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RONALD EARL BAIRD

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS

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THE SYSTEMATICS, DISTRIBUTION, AND ZOOGEOGRAPHY OF THE MARINE HATCHETFISHES (FAMILY STERNOPTYCHIDAE)

RONALD CLAY BAIRD[1]

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[1] Museum of Comparative Zoology, Harvard University, and Marine Science Institute, University of South Florida, St. Petersburg, Fla. 33701.

ABSTRACT

The systematic history of the Sternoptychidae has been one of instability in higher classification. A study of comparative osteology indicates that the hatchetfishes are closely related to the Gonostomatidae but differ from them in certain significant aspects. The Sternoptychidae are therefore given familial rank.

Fossil evidence indicates that the family probably arose during the early Tertiary and reached its present evolutionary grade by the middle Miocene. Three phylogenetically divergent genera are recognized, these being *Argyropelecus*, *Polyipnus*, and *Sternoptyx*, with seven, seventeen, and three species respectively. Many species exhibit geographical variation and morphologically distinct populations were defined in some instances.

The genera differ broadly in habitat as well as morphology. *Argyropelecus* is a high seas pelagic genus limited to the upper 600 m. *Sternoptyx* shows a similar pattern horizontally but inhabits the 500 to 1500 m depth zone. *Polyipnus* occurs only in close association with land, exhibiting a distribution and speciation pattern similar to many tropical shore species. *Argyropelecus* and *Sternoptyx* spe-

cies are seemingly restricted to waters with similar hydrographic and biological properties. Certain species assemblages are used to define zoogeographically distinct areas of the world's oceans.

INTRODUCTION

The systematic history of marine hatchetfishes begins with Hermann's (1781) description of a photophore-bearing fish he called *Sternoptyx diaphana* (from the Greek words "sternon" (chest) and "ptyx" (plate)) and from which the family derives its name. Hermann called attention to the extraordinarily deep and compressed body shape and thus established one of the principal descriptive characteristics of the group. The genus *Argyropelecus* was described by Cocco in 1829 and both genera then appeared in the classic work of Cuvier and Valenciennes (1849).

Günther (1864: 384) placed the above genera in the family Sternoptychidae and included also other midwater genera (presently placed in the family Gonostomatidae) using such characteristics as photophores and gill structures. In addition, *Argyropelecus* and *Sternoptyx* were given subfamilial rank characterized by the presence of a spinous dorsal blade.

Gill (1884), while recognizing that the congener of the Gonostomatine fishes was allied to the Sternoptychidae, nevertheless restricted the family to include only *Sternoptyx* and *Argyropelecus*. He recognized too, a degree of difference between these genera and gave them subfamilial rank.

Günther (1887) added the newly described genus *Polyipnus* to his family Sternoptychidae, which still included the present gonostomatid genera. Goode and Bean (1896) followed Gill in recognizing three families from Günther's one: Gonostomatidae, Maurolicidae, and Sternoptychidae; and in addition, placed the genus *Polyipnus* with the Sternoptychidae. Garman (1899), citing the similarity of the larval forms of Goode and Bean's three families, returned to Günther's original scheme. Brauer (1906: 101) later continued to recognize Günther's classification.

Regan (1923) attempted to clarify the earlier confusion by examining osteological characters, thereby giving more explicit definitions to the taxa. This resulted in assignment of the genera *Sternoptyx, Argyropelecus*, and *Polyipnus* to the family Sternoptychidae, while other related genera were placed in the family Gonostomatidae. Such basic differences as the absence of a basi- and alisphenoid bone in the former family were cited as justification for this split. Regan's classification was later accepted by Norman (1930, 1944) and Berg (1940).

Regan's work did not resolve the problem of family relationship and taxon rank, however. While generally recognizing Regan's classification, Fowler (1936) gave the Maurolicidae familial rank and further complicated the issue by including the genus *Valenciennellus* with Regan's Sternoptychidae. Gregory and Conrad (1936) included *Maurolicus* in the family Sternoptychidae, acknowledging the primitiveness of this genus, as well as its role as a possible congener of Regan's Sternoptychidae. They cited the deep, compressed body form as an evolutionary trend in the family. Smith (1953) essentially returned to Goode and Bean's old classification while Hubbs (1953), referring to the connecting links in the evolution of the Sternoptychidae from the Gonostomatidae, recommended a revival of Günther's classification, thus reducing Regan's Sternoptychidae to subfamilial rank. While Rechnitzer and Böhlke (1958) and Ebeling (1962) have accepted Hubbs' proposal, most modern authors recognize Regan's classification (Schultz, 1961; Morrow, 1964; Backus et al., 1965; Berry and Perkins, 1965). However, Greenwood et al. (1966) indicate that the Sternoptychidae are a specialized offshoot of the Gonostomatidae and, although still recognizing the former as a separate family, they

suspect that further morphological study will support the earlier conclusions of Hubbs.

Historically then, there has been a failure to achieve a stable classification of the Sternoptychidae. The numerous reasons for this failure may be attributed primarily to the use of superficial or highly variable character complexes, the lack of detailed morphological studies using osteological or other acceptable criteria, and subjective conceptual differences concerning the family rank.

The first consideration of a systematic study of the Sternoptychidae must include an attempt to clarify some of the historical confusion. Accordingly, a comparative study of primarily osteological character complexes was undertaken with the following objectives: to help elucidate the family question; to provide characters for explicit definitions of the taxa; and to comment on generic relationships and evolutionary trends among the genera and species complexes. The character complexes cited were sufficiently numerous and functionally distinct to reasonably satisfy the initial objectives. The gonostomatid genera *Maurolicus* and *Valenciennellus* were chosen for comparison with the Sternoptychidae as they are thought, classically, to be most closely related to them, and because any other choice would have to involve a detailed study of the Gonostomatidae.

The use of osteological characters and character complexes as the primary criteria in a systematic study involves the following concepts: 1) The skeletal system is a major constituent of the functional morphology of an individual and should reflect its general evolutionary history. 2) As selection acts on a particular morphological region, it alters the osteology of that region. Both between and within regions, osteological characters may be independent with regard to rate and direction of evolution. 3) The skeletal system is not strictly a single one with a limited function and morphology. Rather, it may be thought of as a series of semi-independent systems or "functional units," each reflecting the functional requirements of that particular unit. 4) An osteological study results in a composite of individual character complexes, some of which may be primitive, others advanced, but which reflect the evolution and specialization within phyletic lines. 5) Osteological characters have been shown to be as consistent as other characters in reflecting phylogeny and evolution. We know more about osteology and its limitations 6) Paleontological evidence is primarily osteological.

Fossil evidence was also considered and a detailed study was made of the fossil record to provide additional information on the evolutionary history and relationships ascertained from the osteological results. After using these in resolving the family question and in presenting an evolutionary history, the various higher taxa were defined and a revision of the respective genera undertaken.

The widespread occurrence and ease of capture of the Sternoptychidae make them ideally suited for studies involving population structure, speciation, and distribution in the midwater or mesopelagic environment. Several recent studies (Haffner, 1952; Ebeling, 1962; Nafpaktitis, 1968) have indicated some of the distributional patterns of certain midwater fishes and the possible factors involved therein. This study attempts to examine some of these factors with regard to present sternoptychid distributions.

METHODS

Material. Because of the vast amount of material examined a detailed list of specimens and stations is not included in this work. Appendix A lists the institutions, vessels, and respective cruises from which material was obtained. A detailed listing of material examined is on permanent file in the Museum of Comparative Zoology, Harvard University.

Collecting and sampling techniques. In a study such as this one, involving material from so many cruises employing a wide variety of gear and using various fishing philosophies, the sources of sampling bias are too numerous to list. However, some of the major problems can be discussed.

Horizontally, there is a marked difference in the amount of sampling between areas. A few areas have been adequately sampled (California, North Atlantic) while others have not been sampled at all. The Pacific in general, the South Atlantic, and the Indian Ocean—especially the southern and eastern portion—are markedly undersampled. The "pseudopelagic" or nearshore midwater environment has not been sampled in most parts of the world. In most cases sampling was seldom extensive enough to appreciate any micro-distributional features or seasonal variation (see Pearcy, 1964).

In addition to differences in collecting gear, there were significant differences in fishing philosophy. Some cruises were faunal surveys with many oblique tows to numerous depths. Other cruises were interested in sampling only over a certain depth range (e. g., upper 500 m), while still others sampled particular environments or collected in sound-scattering layers. The majority of cruises were diurnally biased, collecting primarily in the upper 200 m at night and much deeper during the day. The upper 500 m was much more extensively sampled than deeper waters, especially at depths below 1000 m.

A wide variety of fishing gear was employed. The gear most frequently used was the 10′ Isaacs-Kidd midwater trawl. Many other types of trawls, ring nets, plankton tows, and even dip nets, provided material. Depth determination and data recording varied widely. For example, it was often impossible to tell if a certain sample was a horizontal or oblique tow, or whether the depth recorded was calculated by triangulation or determined electronically with automatic depth recorders. There is an abundance of literature on the problems encountered in sampling midwater organisms from behavioral responses to gear characteristics and performance. For a comprehensive discussion of the problem see Suzuki (1961), Aron (1962), and Harrisson (1967).

Hatchetfishes are easily caught by slow moving towed nets. There is some correlation between size of tow and size of individuals taken. Plankton tows take primarily very small individuals, while 10′ Isaac-Kidd trawls take larger specimens. In general the 10′ IKMT appears to undersample the large individuals, although it does on occasion catch the very largest individuals of a species. Comparisons with catches by the huge Engalls trawl in the northeast Atlantic show that there are more of the larger individuals present than IKMT samples indicate. In the case of *Argyropelecus gigas*, the largest specimens ever recorded were taken in numbers by this trawl. With the exception of *Argyropelecus gigas*, hatchetfishes are small sized and are adequately sampled, except for the largest sizes, by the standard IKMT. Indications are that more work with large midwater trawls, especially those that operate at depths greater than 500 m, will add a new dimension to the "lilliputian" midwater fauna (see Harrisson, 1967: 104).

Measurements and counts. The methods of measurement usually used were those described by Hubbs and Lagler (1947: 13), although the peculiar morphology of the Sternoptychidae necessitated several adjustments. In addition, measurements were adjusted so that in some cases reference points are somewhat different between the genera. Measurements of standard length (SL) and body depth (BD) were made with needle point dividers to the nearest whole millimeter. Other measurements were taken with vernier calipers, and were determined to the nearest tenth of one millimeter.

Characters chosen for measurement were those which appeared to have systematic

importance, or could be directly or indirectly tied to ecological considerations. The following measurements were taken: Standard length—measured from the end of the snout to the farthest extension of the well-marked caudal peduncle (in *Sternoptyx* the peduncle asymmetrical, the lower lobe extends farthest posteriorly). Body depth—in *Argyropelecus* and *Polyipnus* measured from the origin of the dorsal blade to the most ventral extension of body margin, excluding ventral keel scales; in *Sternoptyx* measured from the end of the dorsal fin and essentially a trunk measurement. Dorsal blade—height measured from dorsal body margin to greatest extension of major element in the blade along blade axis (in *Sternoptyx* there is only one element). Jaw length—measured from the point of the retroarticular to the anteriormost extension of the lower jaw. Jaw width—measured in the lateral plane between the left and right lower jaw articulations. Caudal peduncle—a depth measurement across the narrowest dorsal-ventral axis of the caudal peduncle. Abdominal length—used only in *Sternoptyx*, measured from the dorsalmost point of the supra-anal photophore to the posteriormost extension of the caudal peduncle. Supra-abdominal photophore—a *Sternoptyx* character measured from the dorsalmost point of the supra-anal photophore to the dorsal body margin normal to the midabdominal axis. Dorsal fin length—in *Sternoptyx* measured from the origin of the anteriormost fin ray to the origin of the posteriormost fin ray. Orbital diameter—in *Polyipnus* measured along the anterior-posterior axis. Post-temporal spine length—in *Polyipnus* measured from the ventral origin of the spine to its tip. Head length—in *Polyipnus* measured from the end of the snout to the posterior opercular margin. Photophore measurements—measured from the farthest extension of the dark pigmented photophore margins.

The following counts were made. Gill raker number: the number of gill rakers on the first branchial arch of the left side: only clearly defined rakers were counted. Caudal, median, and pectoral ray counts were as per Hubbs and Lagler (1947). Vertebral counts were made from fossils, X-ray photographs, or cleared and stained specimens. Vertebral counts included all separate vertebrae, except the urostylar element(s); vertebral counts for fossil material included only those elements posterior to the major element in the dorsal blade.

Keys and key characters. Because of the damaged condition of many specimens in midwater collections, keys include several characters to aid in identification. Care must be taken when making measurements on, or using key characters with, damaged specimens. Keys were constructed for adults and late juveniles only, and are roughly limited to individuals greater than 20–25 mm in standard length. Photophore complement, especially in the anal series of *Polyipnus*, is complete only in the adults. Most of the key characters are discussed in the descriptions; however, several of the more common ones are expanded as follows. The post-temporal spine in certain species of *Polyipnus* bears small basal spines on its ventral-lateral surface; dorsal, postabdominal, and preopercular spines are often worn or broken, especially in larger individuals. Subcaudal spines appear late in ontogeny and are always small. Spinose borders of the preopercle and ventral keel scales are obvious and well developed. Canine teeth may be missing or broken, but when present they are conspicuously longer than other teeth. Teeth present on the midline of the posterior vomerine shaft in certain species of *Polyipnus* are difficult to see in small specimens. Caudal ray pigment is often reduced by loss or abrasion of the caudal fin. Pigment characteristics used are dark melanistic areas which appear stable in most common preservatives if the specimens are undamaged. Preopercle spine characteristics in the *Argyropelecus lychnus* complex

are sometimes variable, and occasionally borderline cases occur. While keys were constructed for individual identification, population and distribution data should always be checked.

Photophores (Figs. 17 and 18). Photophore nomenclature was adopted from Schultz (1961). The photophore groups are as follows: preorbital (PO)—a single photophore located anterior to the eye (ventrally located in *Sternoptyx*); postorbital (PTO)—a single photophore just posterior to the eye; preopercular (PRO)—a single large photophore located at the ventral margin of the opercular region; subopercular (SO)—a single small photophore at the posterior ventral margin of the opercular region; suprapectoral (SP)—a series of three photophores (two in *Argyropelecus*) in the region above the pectoral fin; branchiostegal (BR)—a cluster or group of photophores located in the branchial region; isthmus (I)—a group of five to six photophores along the anterior ventral body margin below the preopercular complex; abdominal (AB)—a large group of 10–12 photophores along the ventral abdominal body margin; preanal (PAN)—a group of three to five photophores located in the region just above and posterior to the pelvic fins; anal (AN)—a variably numbered group of photophores located along the ventral body margin in the region of the anal fin; subcaudal (SC)—a group of four photophores along the ventral body margin in the region of the caudal peduncle; these usually form a single close-packed cluster but may be separated in certain species of *Argyropelecus*; supra-abdominal (SAB)—(absent in *Sternoptyx*) a series of three (*Polyipnus*) or six (*Argyropelecus*) photophores above the abdominal series along the lateral body margin; supra-anal (SAN)—(absent in *Argyropelecus*) a single photophore in *Sternoptyx* which is anterior to and raised above the anal group; a series of three photophores in *Polyipnus* anterior to and usually raised above the anal group; in certain species the three supra-anal photophores are anterior to but are essentially continuous with the anal series; lateral (L)—a single photophore in the midlateral region of the trunk found only in *Polyipnus*.

Photophore number and position are remarkably constant in the Sternoptychidae. However, rare individuals do have photophores in somewhat abnormal positions or occur with an abnormal number in any group. The number is constant in most photophore groups throughout a genus, although the resultant pattern may be somewhat different owing to differences in body form or photophore location. No sexual dimorphism in photophore number or pattern was observed.

Clearing and staining. For the osteological study, a series of specimens of each species examined was cleared and stained using a slightly modified trypsin digestion technique described by Taylor (1967). This method gave excellent results even on specimens preserved for long periods of time. In addition, the method is considerably more rapid than other techniques. Distorted specimens often gave good results since they were partially relaxed by the digestion process.

Analysis and presentation of data. Because of the magnitude of material examined, computer techniques were employed extensively. Programs (primarily in the Fortran IV language for use with the IBM 7094 at the Harvard University Computation Center) were designed to plot and analyze the data. Four types of data cards were punched and then cross-indexed by cruise and station number. One card contained station location and depth plus hydrographic and time data where available. The catch card incorporated the total catch, the size breakdown of the catch, and other data such as maximum size or size of gravid females. Morphometric and meristic data cards completed the raw data input.

Horizontal distributions were computer

plotted and broken down into three arbitrary, relative abundance categories which were indicated by separate symbols. These plots formed the basis for the distributional charts on each species. Plots of juveniles and gravid females did not differ significantly from overall plots, so they were not included in the data presented.

Depth data were subjected to two separate analyses. The first was a tabular breakdown of all depth data taken primarily by IKMT and in which depth was determined by pressure depth recorders in most cases. Depth figures represent only maximum net depths and in many instances probably represent oblique tows, although where this was definitely indicated oblique tows were excluded. The results are listed in Appendix B. This method was particularly helpful in appreciating sampling bias. For the second analysis, only known horizontal tows were used and a plot of the rate of catch in fish-per-hour against depth was made. Only rates greater than one fish/hour (one-half fish/hour in certain species) were plotted. A much finer definition of the depth range of each species was thus obtained, although the sampling bias cannot be fully ascertained.

Where hydrographic data were available, temperature-salinity plots were made for each species and compared with known water mass T-S envelopes. These plots formed part of the data for Table 24.

Morphometric and meristic data were analyzed using standard statistical methods. All proportional data were computer plotted against standard length, and regression statistics were computed by the least square method. Only adults or late juveniles were used, and relationships were linear in all cases. Variability was quite low in most instances, and as long as stratified samples were taken (covering most of the length range of a species), excellent repeatable regression lines were obtained. Confidence limits decreased with sample size to about 20 individuals, beyond which little reduction could be obtained. Stratified samples as small as eight individuals were adequate to establish good regression lines, which were consistent with larger samples in most cases. In many areas, sample sizes were inadequate and the population parameters presented must be verified further with more sampling. Slope differences were tested statistically and are presented in the various tables. Positional differences between populations could often be detected although the slopes were not statistically different. These, when noted, were plotted (Fig. 23). Meristic data were plotted and a difference of two standard errors on either side of the mean formed the basis for statistical comparison. Dorsal blade height in *Argyropelecus hemigymnus* was plotted in the same manner as meristic data. The slope of blade height to standard length was very low (.008–.02), so that comparisons between individuals over a small length range (22–28 mm) were considered equivalent.

Oceanographic data were obtained from various standard sources (Fuglister, 1960; Sverdrup et al., 1960; Muromtsev, 1963; Schroeder, 1963) and from cruise reports.

OSTEOLOGICAL CHARACTER COMPLEXES

Caudal skeleton (Fig. 1). There is a definite similarity among the caudal skeletons examined. Features in common include: somewhat flattened neural and haemal spines; three characteristic hypural or hypural-like elements in the ventral caudal lobe (definitions and abbreviations of bones follow Norden (1961); see Weitzman (1967a) concerning definition of a hypural element); often one or more post-terminal vertebrae; one or two free epurals (except *Sternoptyx*); and a caudal fin ray count of 10 + 9, with a varying number of dorsal and ventral procurrent rays.

There is considerable variation in the degree of fusion of hypural elements. With the exception of the *Argyropelecus affinis* and *Polyipnus spinosus* species complexes,

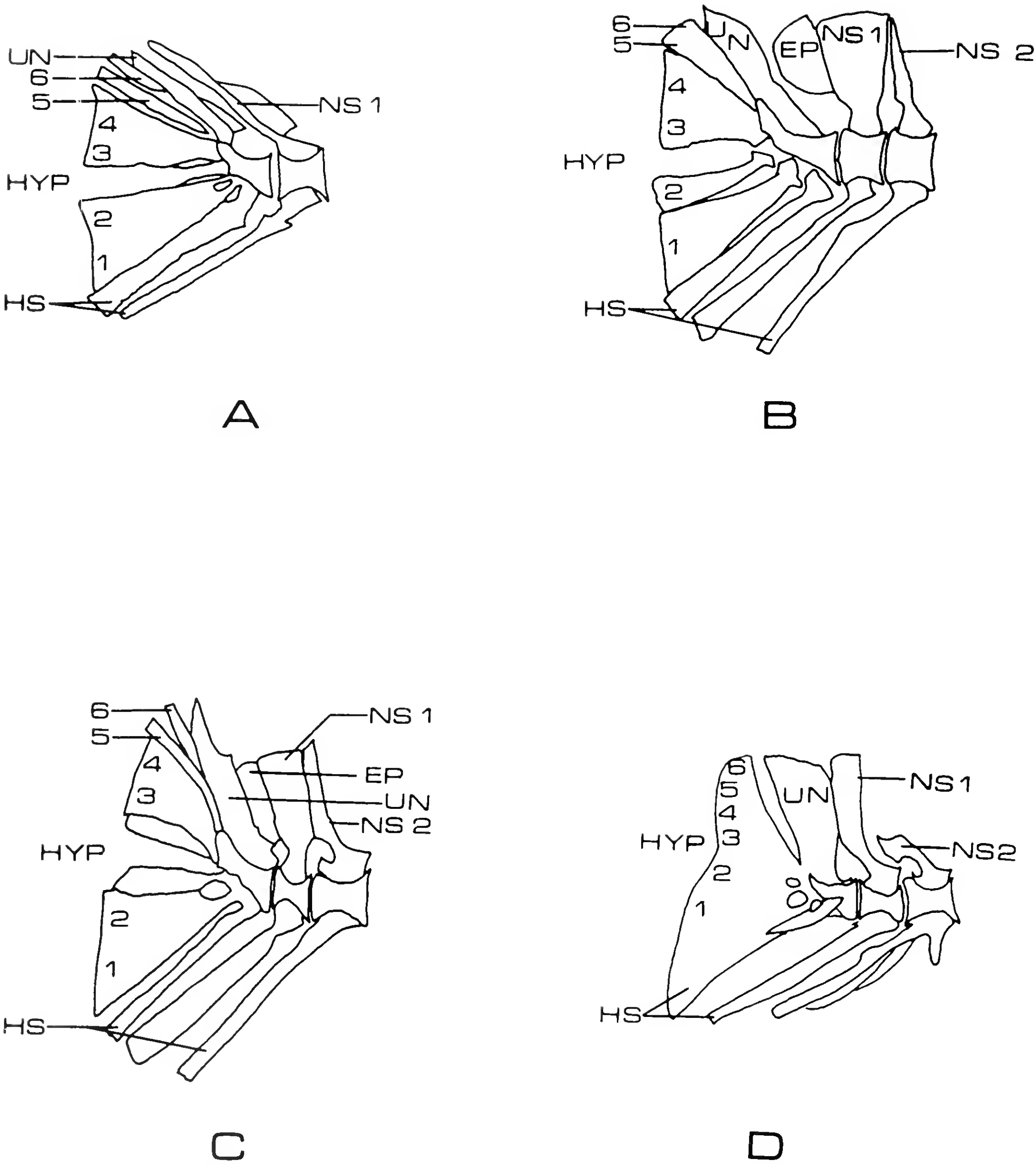


Figure 1. Caudal Skeleton: A. *Maurolicus muelleri*; B. *Argyropelecus affinis*; C. *Polyipnus asteraides*; D. *Sternoptyx pseudobscura*. Abbreviations: EP = epural; HS = haemal spine; HYP = hypurals; NS = neural spines; and UN = uroneural.

hypurals 1–2 and 3–4 are always fused. In some cases, there is complete (*Sternoptyx*) or almost complete (*Valenciennellus*) fusion of hypural elements.

The following are the important evolutionary features. The caudal skeleton of *Maurolicus* appears primitive and is similar to the caudal skeleton of *Vinciguerria* as illustrated by Weitzman (1967b). The three sternoptychid genera are character-

ized by a modification of the first neural spine into a short triangulate, vertical blade. The second neural spine often supports the first. In marked contrast, the gonostomatid genera examined (also *Vinciguerria,* see Weitzman, 1967b) show little modification in this area, and the first neural spine is elongate and forms an integral part of the upper caudal lobe. *Sternoptyx* shows a high degree of specialization with considerable reduction or fusion of elements. *Polyipnus* shares with *Maurolicus* (and *Vinciguerria*) the lack of fusion in hypurals 5 and 6. In some respects *Polyipnus* resembles the gonostomatid genera examined in size and shape of the uroneurals although, in general, it appears similar to *Argyropelecus.*

Axial skeleton (Figs. 8–11). While there is a similarity in structure and appearance of the vertebral centra in all genera examined, there are differences in neural and haemal spine pattern and structure. Posteriorly, the haemal and neural spine arrangement is symmetrical in all cases. In *Maurolicus* and *Valenciennellus* both spines are relatively long, unflattened, and tapering. The sternoptychid genera show a definite broadened and flattened condition particularly evident at the distal end. *Polyipnus* and *Argyropelecus* are alike in this respect. *Sternoptyx,* with considerable elongation of the posterior neural and haemal spines, reflects an independent and highly modified condition. *Vinciguerria* (Ahlstrom and Counts, 1958) appears more similar to *Polyipnus* than either of the gonostomatids examined.

Anteriorly, the symmetrical pattern of haemal and neural spines continues in *Valenciennellus* with no marked transitional region. However, in *Maurolicus* and the Sternoptychidae, there is an area of transitional vertebrae which is peculiar. There is a reduced, although fully formed, plural rib-bearing member followed by a number of characteristic haemal spines which may or may not be arched. This series of spines carries at least one pair

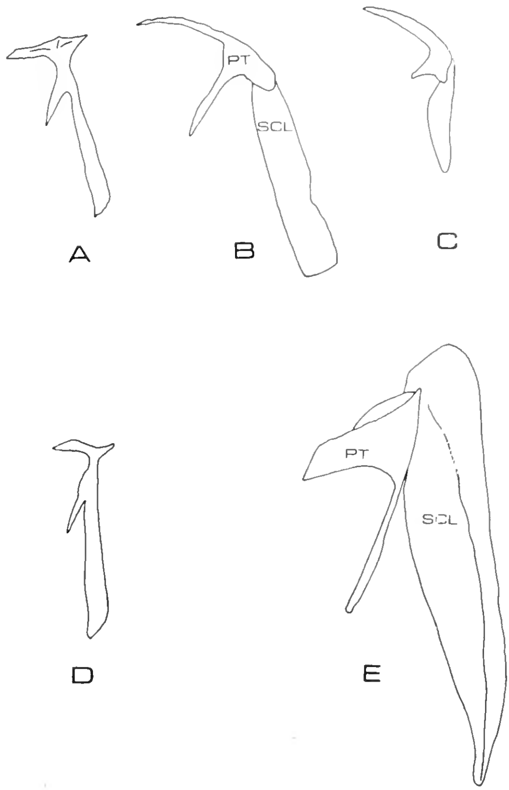


Figure 2. Post-temporal and supracleithrum: A. *Argyropelecus aculeatus;* B. *Maurolicus muelleri;* C. *Valenciennellus tripunctulatus;* D. *Polyipnus asteroides;* E. *Sternoptyx pseudobscura.* Abbreviations: PT = post-temporal; SCL = supracleithrum.

of greatly reduced or vestigial ribs. In *Maurolicus,* the first arched haemal spine is somewhat flattened distally. *Polyipnus* and *Argyropelecus* show a marked broadening of the distal end of these anterior haemal spines, with an increase in length proceeding posteriorly. *Sternoptyx* has a shortened flat first haemal spine; however, the posterior spines are elongate and not characteristically flattened.

The neural spines posteriorly are long, thin, and tapering in *Maurolicus* and *Valenciennellus.* As before, the sternoptychids show a broadened pattern unlike the above gonostomatids. *Polyipnus* and *Argyropelecus* are remarkably similar in this region.

The articulation of ribs is similar in all species, as well as the presence of reduced or vestigial pleural ribs, probably an indication that many more centra were rib-bearing in more primitive forms (see Weitzman, 1967b: 518). *Maurolicus* has a higher number of pleural and reduced pleural ribs than the sternoptychids. The latter are quite distinctly separated from *Maurolicus* and *Valenciennellus* by the presence of six or seven greatly broadened and lengthened pleural ribs which form a heavy protective cage around the now expanded visceral cavity. The number of abdominal vertebrae (the first caudal vertebra is defined as the anteriormost vertebra with a complete haemal arch) is relatively constant in the *Sternoptychidae* at about eleven (one specimen of *Polyipnus asteroides* had ten; Kotthaus (1967) reports twelve for *P. meteori*). Sample sizes were small, however.

Dorsal blade (Figs. 8–11). Weitzman (1967b) reported that the anteriormost pterygiophore of the dorsal fin consists of at least two fused pterygiophores in *Vinciguerria*. This same characteristic is found in *Maurolicus* which, in addition, has a number of pterygiophores that do not bear fin rays anterior to the fused one. The sternoptychids have this same basic feature, but have further modified it into essentially a "spinous dorsal." In *Polyipnus*, the fused pterygiophore is extended above the dorsal body surface and is spinose at the distal end. The anteriormost pterygiophores are enlarged, and closer together and more extensively allied to the supporting neural spines than they are in *Maurolicus*. These anterior pterygiophores become even more enlarged and closely allied, extend further above the dorsal surface, and with the fused pterygiophore form an extensive, sharp, dorsal blade in *Argyropelecus*. *Sternoptyx* retains the *Maurolicus* configuration anteriorly, but the fused pterygiophore becomes considerably extended and modified into a large dorsal spine.

Pelvic girdle (Figs. 8–11). In *Maurolicus* (also *Vinciguerria*, Weitzman, 1967b), the basipterygia are located even with or below the ventral margin of the pleural ribs. The paired basipterygia lie almost horizontally above the ventral body surface and are not closely joined to any rib element. With the broadening and deepening of the anterior thoracic region in the sternoptychids, the pelvic girdle has become a major structural element for the midregion of the trunk. *Polyipnus* exhibits a more intermediate condition than *Sternoptyx* and *Argyropelecus*. In the former, the basipterygia are oriented at approximately 45° to the ventral body surface and are located between the posteriormost large pleural ribs. There is now a relatively long ventral extension which ends in a spine protruding below the ventral body surface. The pattern becomes more pronounced in *Argyropelecus*. In this instance, the basipterygia are closely allied to each other and to the posteriormost large pleural rib. In some cases, the basipterygia are fused (*A. hemigymnus*) and the last pleural rib may become further enlarged for support (*A. aculeatus*). The ventral spiny process has also become more pronounced. *Sternoptyx* exhibits essentially the same evolutionary trend as *Argyropelecus*, with the fused basipterygia extending dorsally for a considerable length along the pleural ribs.

Pectoral girdle (Figs. 8–11). The pectoral elements, their general location and shape, are similar in all genera examined and include a well-developed mesocoracoid (see Weitzman, 1967b: 519). *Polyipnus* and *Argyropelecus* have an extended posterior flange of the cleithrum which protects and strengthens the pectoral area. The ventral margin of this flange has a characteristic spinose edge. The flange is noticeably reduced in *Sternoptyx*.

A forked post-temporal and well-developed supracleithrum are present in all genera (Fig. 2). *Polyipnus* and *Argyropelecus* are unique in that these two bones

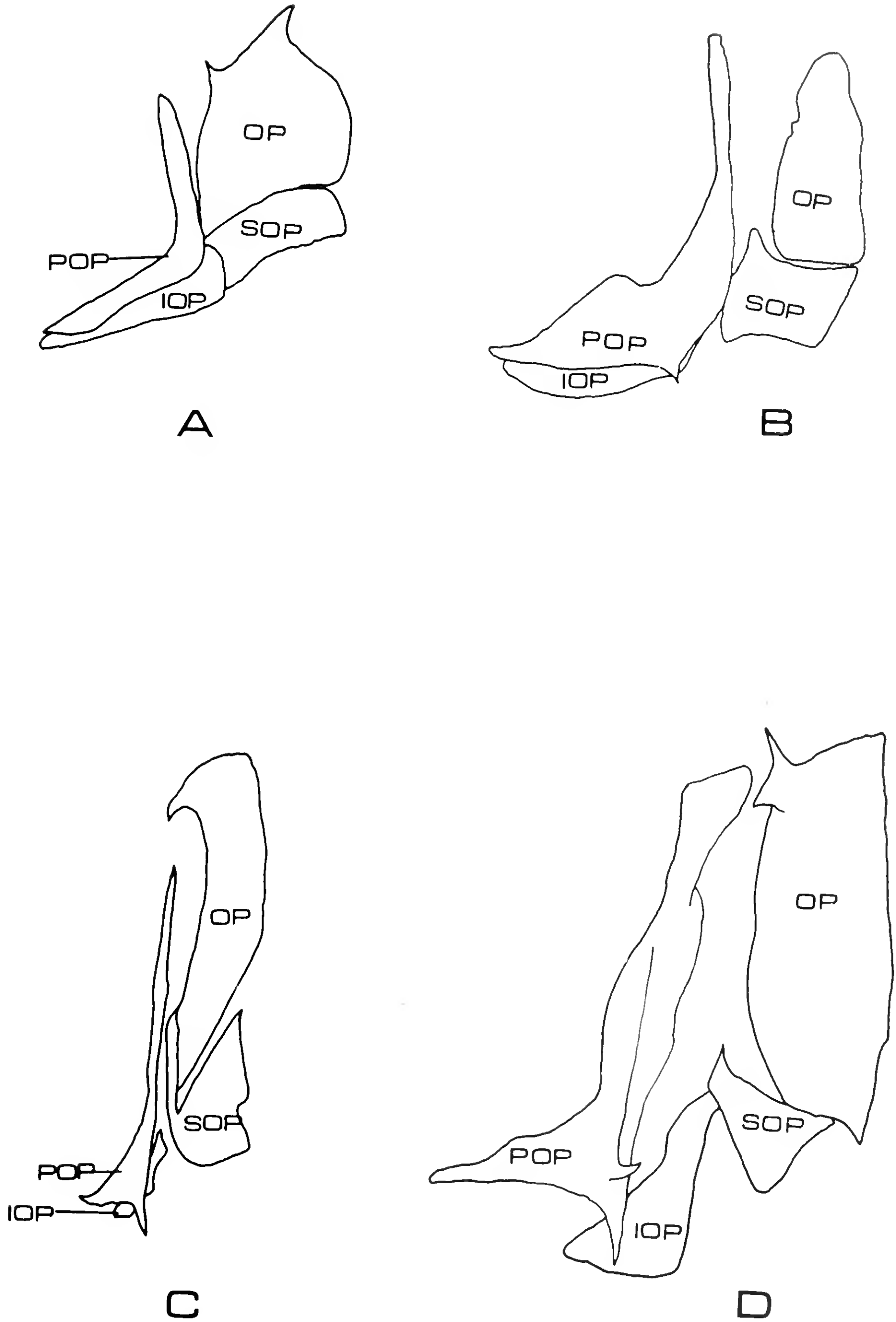


Figure 3. Opercular Series: A. *Maurolicus muelleri*; B. *Polyipnus asteroides*; C. *Sternoptyx pseudobscura*; D. *Argyropelecus hemigymnus*. Abbreviations: IOP = interopercle; OP = opercle; POP = preopercle; SOP = subopercle.

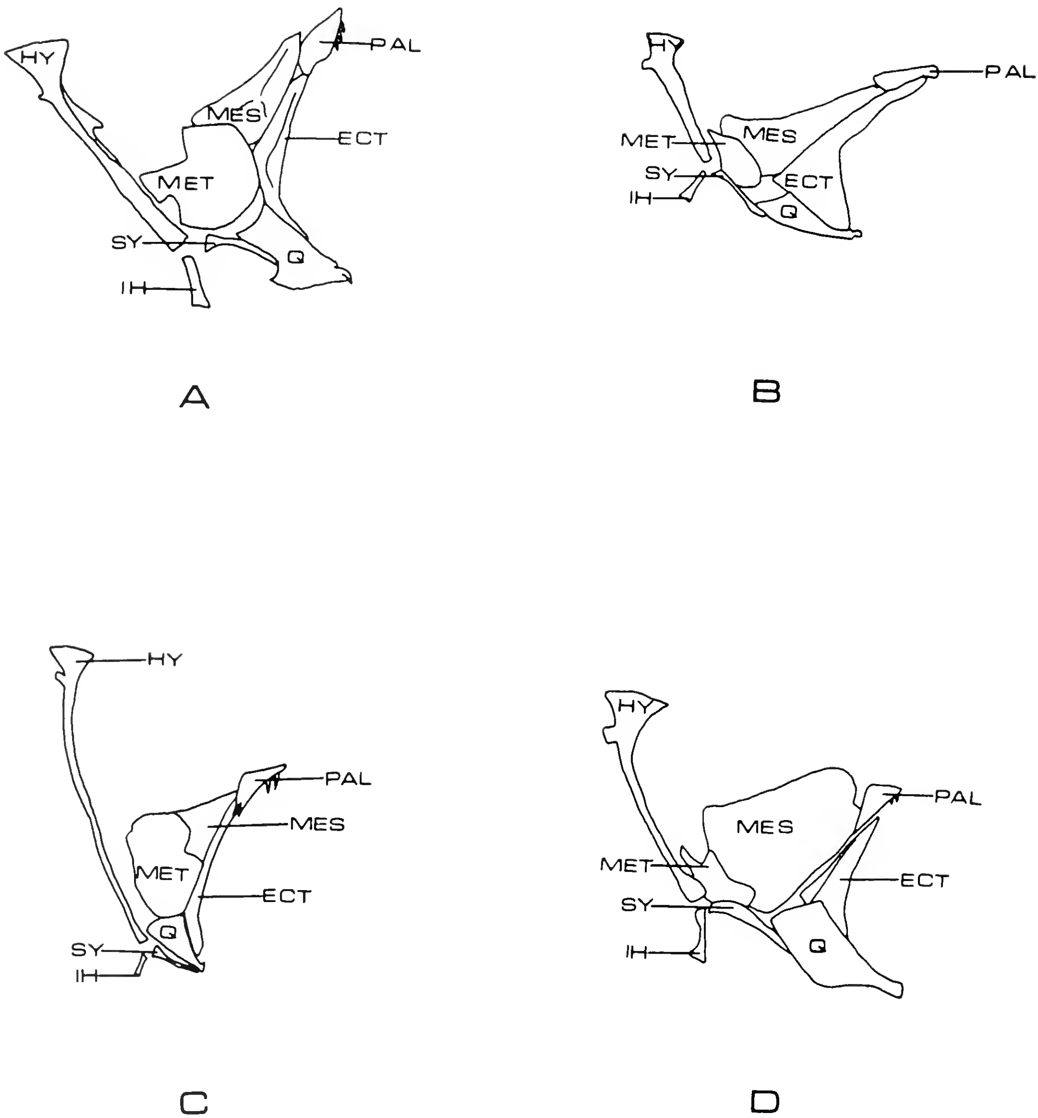


Figure 4. Suspensarium: A. *Polyipnus asteroides*; B. *Maurolicus muelleri*; C. *Sternoptyx pseudobscura*; D. *Argyropelecus hemigymnus*. Abbreviations: ECT = ectopterygoid; HY = hyomandibular; IH = interhyal; MES = mesopterygoid; MET = metapterygoid; PAL = palatine; Q = quadrate; SY = symplectic.

are fused. The post-temporal half of this process extends posteriorly above the dorsal body margin and bears spines. In certain species of *Polyipnus* these spines may become quite elaborate. In *Sternoptyx*, which has no such fusion, the post-temporal is forked and enlarged, and the whole structure reflects a different evolutionary development.

Opercular series (Fig. 3). There is a classic opercular series present in the genera examined, with an interopercle below the ventral margin of the preopercle. There appears to be an evolutionary trend

from *Maurolicus* through *Polyipnus* to *Argyropelecus*. In *Polyipnus*, the interopercle is similar in shape to *Maurolicus*, but somewhat less broad. The preopercle has developed a ventral spine. A reduction in the anterior process of the interopercle, which now covers only the posterior ventral margin of the preopercle, may be observed in *Argyropelecus*. The preopercle, while similar in form to *Polyipnus*, has a lateral spine in addition to the ventral. *Sternoptyx* is somewhat independently modified with elongation and reshaping of the opercle and preopercle. The interopercle is similar to *Argyropelecus*, and the preopercle has a single ventral spine.

Upper jaw. The upper jaw, considering its close relation to feeding ecology, is somewhat similar in *Maurolicus, Polyipnus*, and *Argyropelecus*. There are two characteristically shaped supramaxillae, a well-developed toothed maxilla and premaxilla. The premaxillae have short ascending processes (as does *Vinciguerria*). The maxilla, included in the gape to a small degree, is markedly broadened posteriorly in *Polyipnus*, and the whole jaw apparatus reflects a peculiar method of feeding. *Sternoptyx* is quite different. In this instance the maxilla is heavily toothed and the major upper jaw bone in the gape. The premaxilla is small, although toothed, and has no ascending process. The second supramaxilla has been lost.

Suspensorium (Fig. 4). There appears to be a general evolutionary trend in the Sternoptychidae in which the suspensorium migrates from behind and slightly below the posterior orbital region, ventrally and anteriorly to a point directly below the anterior half of the orbit. This trend can be seen by examining the ratio of quadrate length to hyomandibular length: *Maurolicus*, 1:1.25; *Polyipnus*, 1:1.5; *Argyropelecus*, 1:2.5; *Sternoptyx*, 1:7.4. The metapterygoid bone is proportionately smaller in *Maurolicus* and *Polyipnus*, and the mesopterygoid is greatly enlarged in the latter. This again reflects the peculiar jaw morphology in this genus.

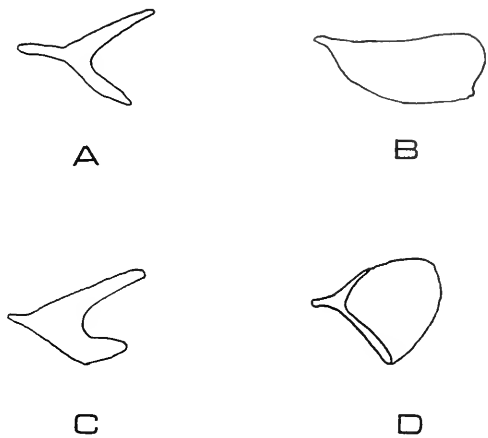


Figure 5. Urohyal: A. *Sternoptyx pseudobscura*; B. *Maurolicus muelleri*; C. *Argyropelecus sladeni*; D. *Polyipnus asteroides*.

Hyoid (Fig. 5). The most notable hyoid feature is the gradual reduction of the platelike posterior extension of the urohyal in the sternoptychids. *Polyipnus* illustrates an intermediate condition, while *Sternoptyx* and *Argyropelecus* show complete reduction to a Y-shaped bone.

Chondrocranium. The curvature of the parasphenoid exhibits a continuous gradation from a nearly horizontal position in *Maurolicus* to the extreme right-angled bone in *Sternoptyx*. The presence and degree of ossification of the basisphenoid is variable. It is well developed and has two centers of ossification in *Valenciennellus*. Only the dorsal ossification remains in *Maurolicus*, while the bone is absent in *Argyropelecus*. *Polyipnus* and *Sternoptyx* have well-developed basisphenoid bones.

The neurocranium (Fig. 6) is generally conservative when viewed as a whole. The shape, relative size, and location of the bones are similar in all genera examined. The neurocranium resembles *Vinciguerria* (Weitzman, 1967b), especially in the general shape and location of the sphenotics, pterotics, and epiotics. Important features

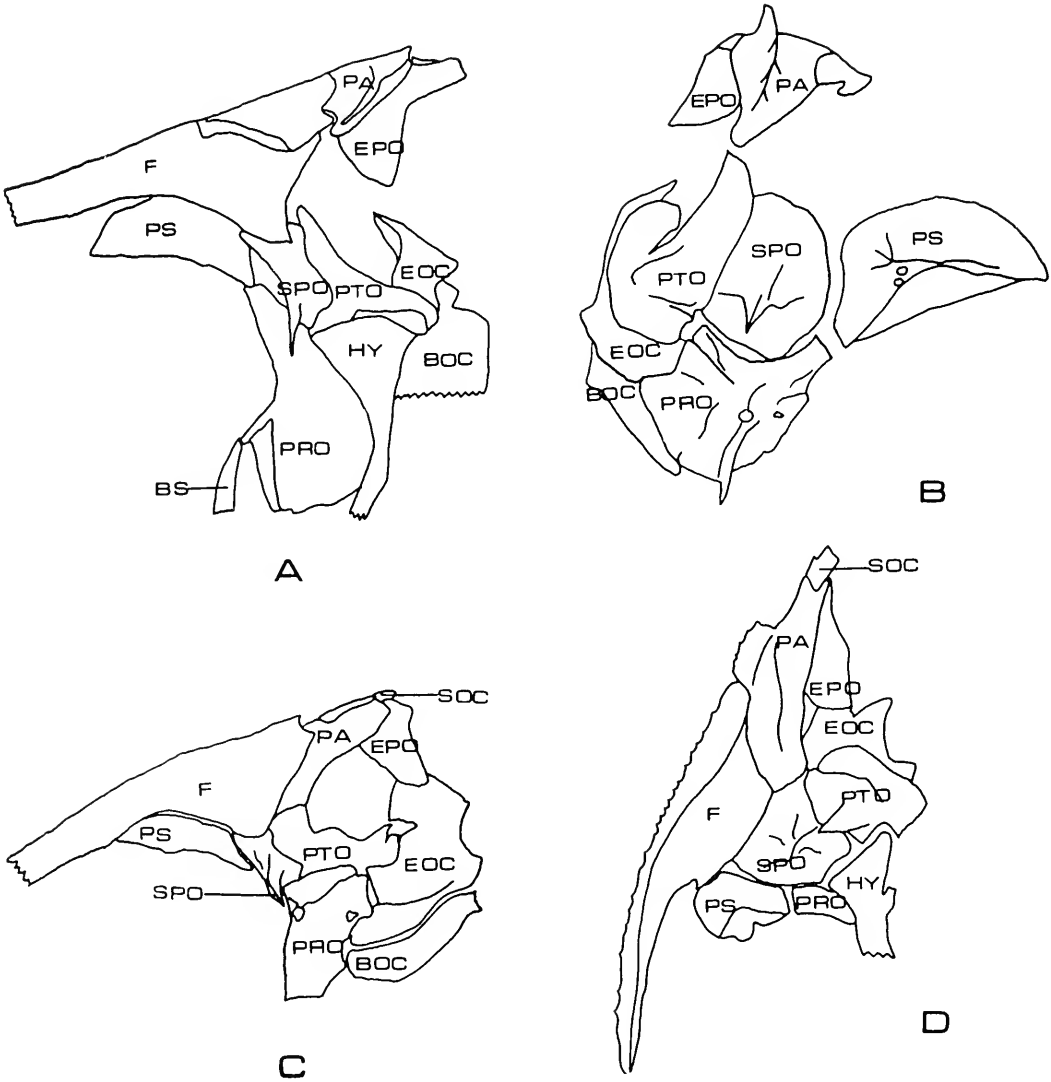


Figure 6. Neurocranium (lateral view): A. *Polyipnus asteroides;* B. *Argyropelecus hemigymnus* (frontals removed); C. *Maurolicus pennanti;* D. *Sternoptyx pseudobscura.* Abbreviations: BOC = basioccipital; BS = basisphenoid; EOC = exoccipital; EPO = epiotic; F = frontal; HY = hyomandibular; PA = parietal; PRO = prootic; PS = pterosphenoid; PTO = pterotic; SOC = supraoccipital; SPO = sphenotic.

are: the epiotics meet below the supraoccipital in sternoptychids, while there is no tendency in this direction in *Maurolicus* and *Valenciennellus* (Fig. 7); the presence of well-developed parietals with dorsolateral ridges in sternoptychids, but not in other genera examined; the presence of a well-developed alisphenoid (pterosphenoid) bone in all genera; and the progressive tendency for the neurocranial axis, as measured along the frontal, to assume a more vertical configuration from *Polyipnus* to *Sternoptyx*. There is considerable development of the otic region in *Polyipnus*

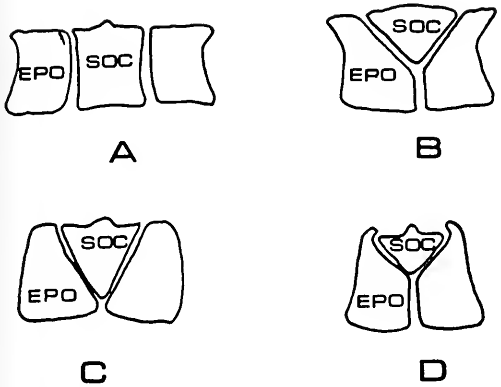


Figure 7. Epiotic-Supraoccipital Relationship (posterior view): A. *Maurolicus muelleri;* B. *Polyipnus osteroides;* C. *Sternoptyx pseudobscura;* D. *Argyropelecus hemigymnus.* Abbreviations: EPO = epiotic; SOC = supraoccipital.

which contains peculiarly shaped and very large otoliths (Kotthaus, 1967).

Abdominal keel scales (Figs. 8–11). *Polyipnus* and *Argyropelecus* have developed ossified plates (modified scales) which form a keel and serve to give structure to the abdominal region and associated photophore groups. Several plates appear posterior to the pelvic fins; most are anterior to them. The plate size, number, and distance between plates is less well developed in *Polyipnus. Sternoptyx* seems also to have a keel-like structure, but this is not ossified. The gonostomatids examined have little keel development and no ossification in this region.

Anal pterygiophores (Figs. 8–11). In sternoptychids, the anal pterygiophores show a characteristic gap. Several pterygiophores are associated with and between the same haemal spine forming a circular gap. In this respect the *P. spinosus* species complex is the least well developed. In the gonostomatids examined there is one pterygiophore for each haemal spine with no gap. The anteriormost anal pterygiophore possesses flangelike processes projecting laterally in *Polyipnus, Sternoptyx,* and *Maurolicus.* The former two have, in addition, pronounced ventral processes lacking in *Maurolicus. Argyropelecus* has no processes, although the anal pterygiophores are enlarged.

Photophores. The glandular nature and pattern of photophores seem to indicate some relationship among all genera studied. The trend appears to be from a condition of an essentially unbroken row of photophores on the ventral body surface (*Maurolicus*) to one in which this row is broken both horizontally and vertically (sternoptychids). As before, *Polyipnus* is intermediate in this respect.

OSTEOLOGICAL CONCLUSIONS

The osteological results lead to the following conclusions. The present definitions of the family (e. g., Regan, 1923; Schultz, 1961; and Morrow, 1964) and included genera are inadequate, often seriously in error, and require revision. The Sternoptychidae appear to be derived from some antecedent of the primitive genus *Maurolicus.* The genera *Sternoptyx, Argyropelecus,* and *Polyipnus* form a separate taxon. Each of these genera has probably been distinct for a long period, as each shows a great deal of divergence and independent evolution.

From the evidence above there is little doubt that the two maurolicid genera and the Sternoptychidae are closely related. The traditional differences such as absence of a mesocoracoid and alisphenoid (pterosphenoid), curved parasphenoid, and even the particulars of the dorsal blade have been found to be, wholly or in part, similarities rather than differences. Basic differences do exist, however, and in general follow from Hermann's original characterization of the Sternoptychidae as fish having a deep, highly compressed body form. It is this striking evolutionary pattern that gives rise to many of the following character complexes which separate the present Sternoptychidae from those gonostomatids examined.

1. Modification of the first neural spine, appearing as a short, triangulate, vertical blade with further modification of the

Figure 8. *Maurolicus muelleri*: R/V CHAIN, Cruise 17, RHB 804; 10° 52′ N; 29° 26′ W.

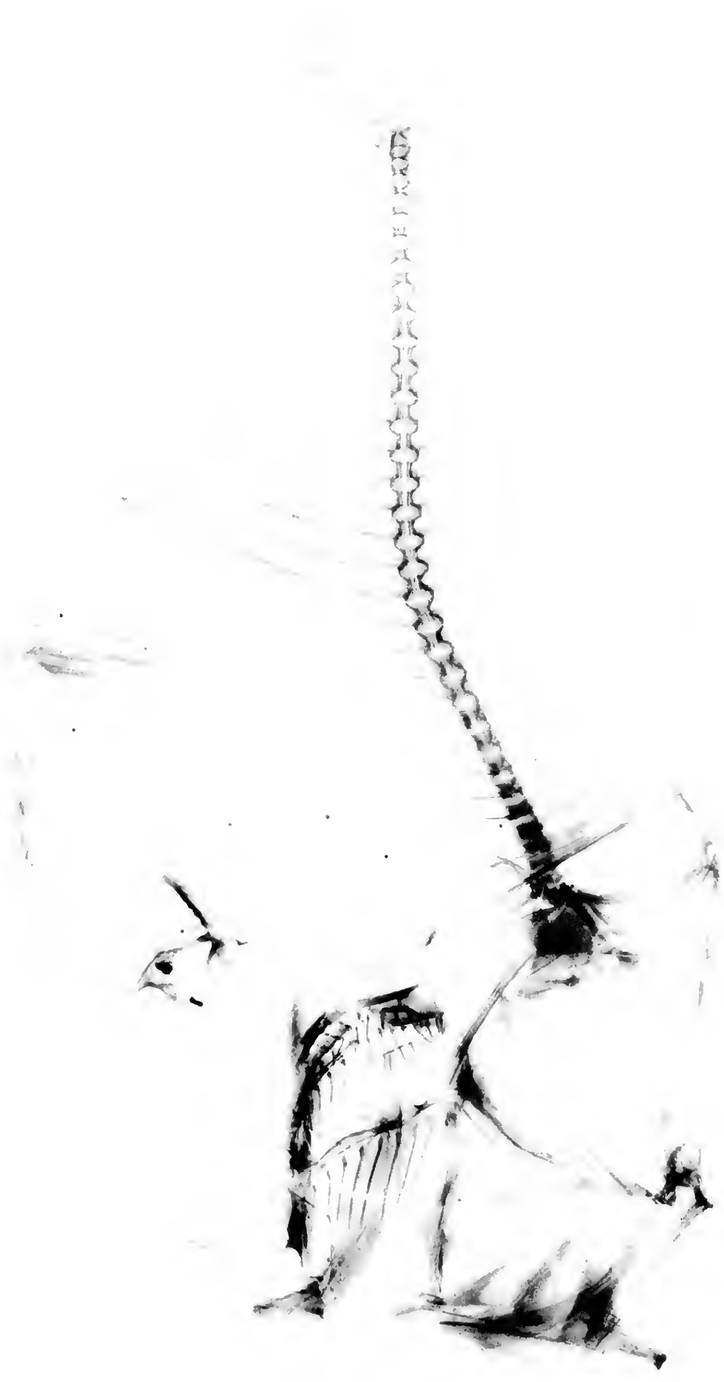


Figure 9. *Polyipnus asteroides:* R/V CHAIN, Cruise 60, RHB 1295; 22° 22′ N; 95° 20′ W.

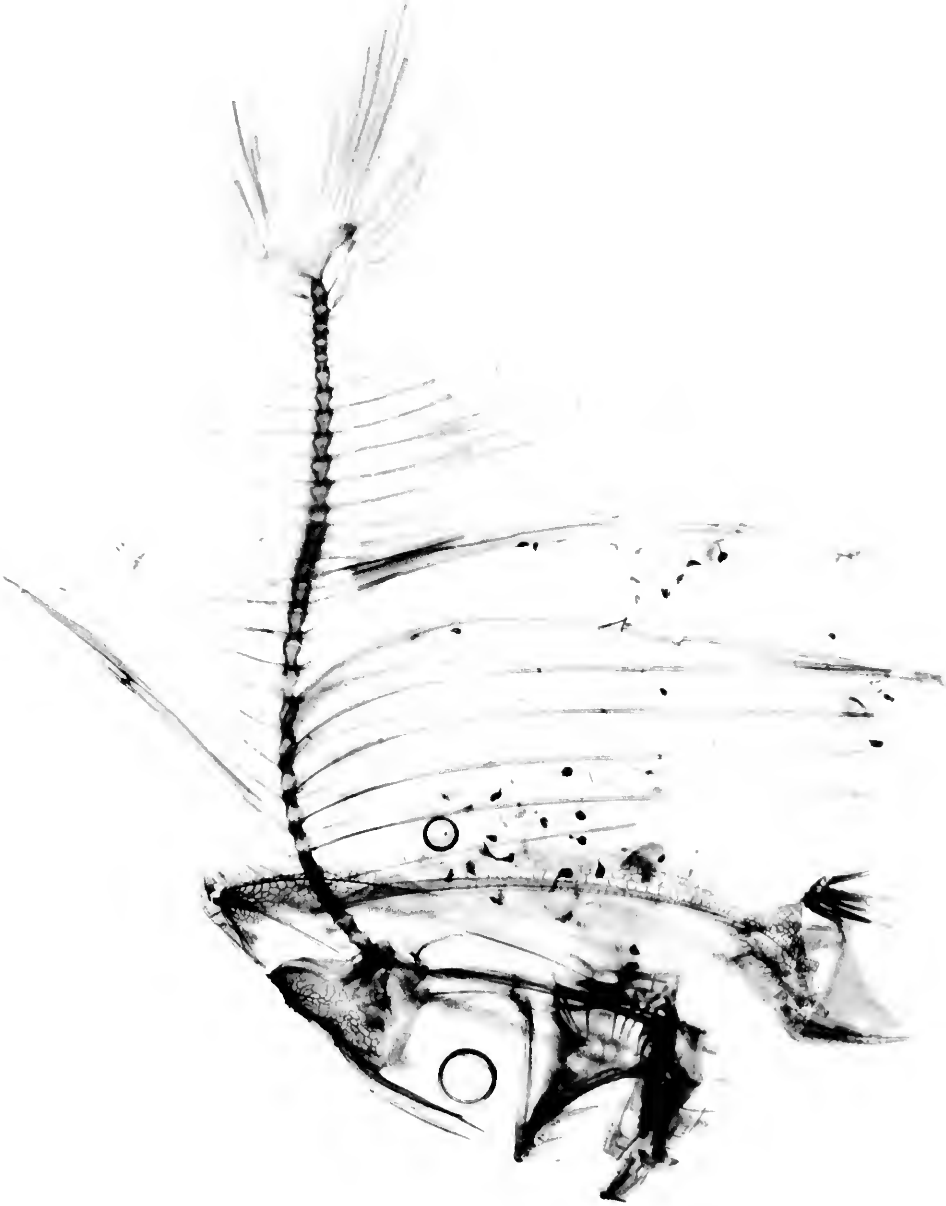


Figure 10. *Sternoptyx pseudobscura:* R/V CHAIN, Cruise 35, RHB 977; 01° 20′ S; 27° 37′ W.

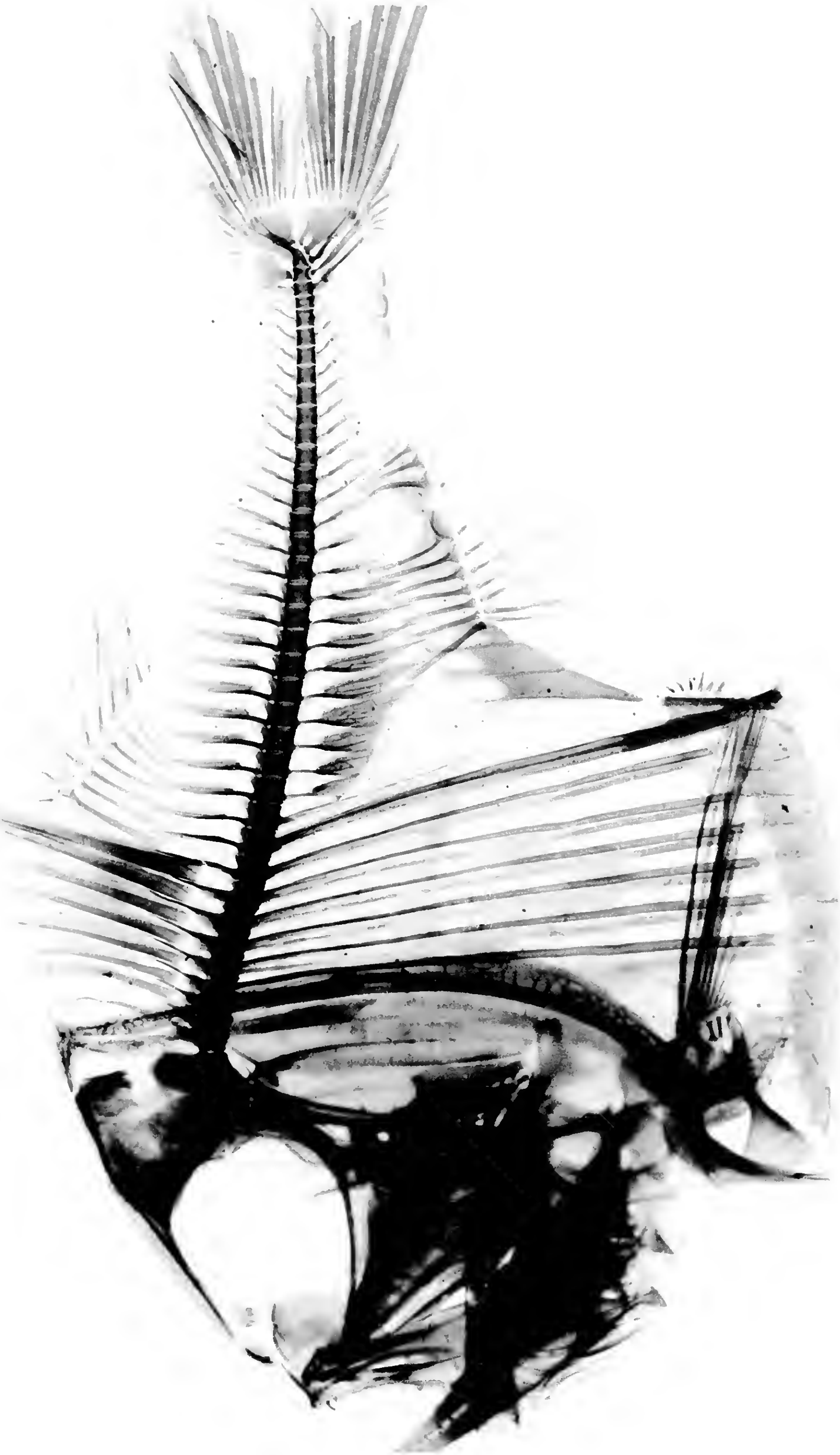


Figure 11. *Argyropelecus olfersi*: USNS ELTANNIN, Station 1769; 36° 05′ S; 133° 00′ W.

second neural spine to serve as a supporting element. (In the *P. spinosus* species complex, the second neural spine resembles the first.)

2. Characteristic broadening and flattening of the haemal and neural spines in the posterior caudal region.

3. The presence of six or seven large, heavy, pleural ribs with relatively few reduced or vestigial ribs. This includes a low number (10–12) of abdominal vertebrae.

4. Development of the dorsal pterygiophore system into a "blade" or spine.

5. A vertically oriented pelvic girdle, the basipterygia bearing spines, sometimes fused, and closely allied to the heavy pleural ribs.

6. A preopercle with a well-developed ventral spine.

7. A heavy, forked, post-temporal which is fused to the supracleithrum in *Argyropelecus* and *Polyipnus*, forming a spiny extension dorsally.

8. A progressive migration forward of the suspensorium.

9. Reduction of the bony extension of the urohyal.

10. Epiotics meeting below the supraoccipital and the presence of well-developed, ridged parietals.

11. Presence of a well-developed abdominal keel-like structure which is ossified in *Argyropelecus* and *Polyipnus*.

12. Presence of a circular gap in the anal pterygiophore series, these pterygiophores being enlarged.

13. Presence of ventral processes on the anteriormost anal pterygiophore in *Sternoptyx* and *Polyipnus*.

14. Marked similarity of photophore pattern and number.

Some of these character complexes are not radically different from the gonostomatids examined, and there is a degree of convergence and parallel evolution which is difficult to appraise. Taken as a whole, however, they strongly suggest that the sternoptychid genera have reached a common evolutionary grade, typified by their peculiar body form, and by which they differ from the more generalized and primitive maurolicid gonostomatids.

While acknowledging that the Sternoptychidae are a specialized offshoot of maurolicid or premaurolicid stock, for the following reasons I do not feel justified in combining the Gonostomatidae and Sternoptychidae as some have suggested.

The present family Gonostomatidae is an unwieldy one which involves many diverse types and requires extensive revision (Weitzman, personal conversation). The problem of gaps, their size and importance, cannot be adequately answered without further study within the Gonostomatidae. Osteologically, the Sternoptychidae have reached an evolutionary grade peculiar to themselves and one quite distinct in several major ways from the gonostomatids examined. Using for a guideline the family concept as it is generally employed by Mayr, Linsley, and Usinger (1953), it appears that the Sternoptychidae do have an ecological, or at least adaptive, distinctness.

The adaptive distinctness concerns the peculiar body shape and its possible functional significance. There are at least two major adaptive features involved. The first deals with the ideas and evidence presented by Denton and Nicol (1965) and Nicol (1967) on the relationship between silvery color and body shape in teleost fishes. The midwater environment is one in which the distribution of daylight is independent of the altitude of the sun and cloudiness of the sky, and light distribution is essentially symmetrical about a vertical to the surface. Furthermore, the Sternoptychidae have brilliant, silvery sides. All fish species with these features so far examined (Denton and Nicol, 1965; Nicol, 1967) have layers of reflecting platelets which are oriented to make the fish as invisible as possible. It may be assumed that the same is true with hatchetfish. There is a change in reflectivity with body rotation in the several Sternoptychid

species examined. A silvery fish which is flattened laterally, having very little inclined ventral surface will approach the ideal in camouflaging (see Denton and Nicol, 1965: 717). The Sternoptychidae could thus serve as a living model for such a body form.

The second adaptive feature concerning body shape is the development of heavy structural ossifications and spines, especially the dorsal "blade." Spines have developed in fish, presumably, for protection. The sternoptychids have several extensive spine complexes: post-abdominal, post-temporal, preopercle, and dorsal. The spines are rigidly braced and the whole body strongly ossified, resulting in a compact rigid body shape. A spinous dorsal has developed somewhat analogous to that of the higher Perciform fishes. This, coupled with the expanded abdominal region, results in a high length-to-depth ratio (Table 1).

In an environment populated by a host of predators, many with special adaptations for ingesting large prey items, an increase in the length-to-depth ratio of a prey should be advantageous. A predator normally capable of swallowing *Valenciennellus* would require an approximate threefold increase in mouth diameter in order to accommodate *A. hemigymnus* of the same length (Table 1). Ossification also takes place quite early. Juveniles or prejuveniles of about 10 mm have well-developed spines and are ossified.

Phylogenetic relationships. The question of a monophyletic origin of the hatchetfish is unanswerable. The three genera show a great deal of divergence and independent evolution even within genera. Using the character complexes examined, some comments about generic relationships can be made, however.

The family appears primitive and probably originated from a premaurolicid ancestor, possibly something between the very early *Vinciguerria* and *Maurolicus*. Most of the characters examined could have been derived from a form somewhat intermediate to the above genera.

The genus *Sternoptyx* seems to have diverged quite early from the line or lines leading to *Polyipnus* and *Argyropelecus*. It then continued to evolve independently, resulting in the present highly specialized form. In almost every case, *Sternoptyx* shows marked differences. The presence of a basisphenoid, the characteristically shaped, enlarged, first anal pterygiophore; the simple anterior, dorsal pterygiophores; possibly the meeting of the parietals, and the unfused post-temporal and supracleithrum all appear primitive. These characters are also shared with *Polyipnus* with the exception of the unfused post-temporals and meeting parietals. The presence of a small premaxilla and large maxilla as the major jaw bone in the gape are generally regarded as primitive. However, jaws and dentition have varied considerably in gonostomatids (Grey, 1964), and this may be a secondary phenomenon. The disappearance of the anterior pedicels of the premaxilla and loss of the second supramaxilla can be explained in the same way, especially since the orbital region seems to have undergone considerable expansion. The resemblance of the urohyal to *Argyropelecus* may again be the result of parallel or convergent evolution involving feeding ecology which is similar in these genera.

Evolution from a premaurolicid ancestor can be traced somewhat more directly in the case of *Polyipnus* and *Argyropelecus*. *Polyipnus* and *Argyropelecus* share several character complexes: the characteristic blade-shaped, caudal haemal spines; the presence of the double pterygiophore as the major element in the "blade"; the presence of ossified, bony keel plates; the fusion of the post-temporal and supracleithrum; and separation of parietals by the supraoccipital (known to be variable in the Gonostomatidae). *Polyipnus* appears intermediate between *Maurolicus* and *Argyropelecus* in several characters:

TABLE 1. BODY DEPTH AND STANDARD LENGTH MEASUREMENTS.

Family	Species	SL (mm)	Maximum Body Depth* (mm)
Gonostomatidae	*Danaphos aculatus*	38.0	9.2
	Valenciennellus tripunctatus	26.0	5.4
Sternoptychidae	*Argyropelecus hemigymus*	38.0	24.0
	Argyropelecus hemigymnus	26.0	16.9

* Includes dorsal blade.

the axial skeleton in general; anterior dorsal pterygiophore development; pelvic girdle modification; evolution of the cleithrum, first branchiostegal rays, and urohyal; the opercular series, especially the preopercle and interopercle; suspensorium development; parasphenoid curvature, and progressive deepening and shortening of the body with reduction in a long unbroken series of ventral photophores. *Polyipnus* has characters that are not shared with *Argyropelecus* in addition to those which are shared with *Sternoptyx*. These include: hypurals 5 and 6 unfused (3 and 4 also in the *P. spinosus* complex); small, relatively unmodified dentition; and, a urostylar element with several unfused post-terminal centra.

Polyipnus also has several highly specialized characters: the peculiar jaw morphology; a greatly enlarged otic region with characteristically shaped, large otoliths (Kotthaus, 1967); and, the peculiar development of the cleithrum (pectoral shield).

The divergence of *Polyipnus* and *Argyropelecus* has involved the continued evolution of many intermediate characters mentioned above. Other major developments in *Argyropelecus* are: fusion of hypurals 5 and 6 and the post-terminal centra; the presence of seven rather than six heavy pleural ribs; development of a lateral preopercular spine (one species of *Polyipnus* has this); development of a fanglike dentition; loss of the basisphenoid; loss of the flangelike process on the first anal pterygiophore; and, the development of telescopic eyes.

Because the number of character complexes examined was limited, the suggested phylogeny is only a tentative one. The family consists of three divergent, independently specialized genera. *Polyipnus* appears the most primitive, *Sternoptyx* the most highly specialized and the most difficult to place, while *Argyropelecus* falls somewhere in between.

THE FOSSIL RECORD

The earliest reported sternoptychid fossil is from the Eocene of the Dabakhan beds of Georgia, USSR (Daniltshenko, 1962). The fossil, *Polyipnoides levis,* is not well preserved and many important characters cannot be appraised. It does have long pleural ribs and a characteristic broadening of the body anteriorly. The post-temporal, however, is unlike any modern sternoptychid. The dorsal "blade" or pterygiophore development is absent and the jaws seem more gonostomatidlike, although this is difficult to determine with certainty. The neural and haemal spines show little characteristic flattening, and the frontals do not exhibit the heavy development characteristic of the hatchetfish. Consequently, it appears that while this fossil could be a proto-sternoptychid fish, I cannot accurately place it with the present Sternoptychidae or Gonostomatidae.

Polyipnus sobnioviensis was repórted from the Jaslo shales of Poland (Jerzmańska, 1960; Jerzmańska and Jucha, 1963) and dates as late Eocene–early Oligocene. Enlarged pleural ribs with a general broadening of the body anteriorly are present in this species. Pterygiophore development

anterior to the dorsal fin rays is definite, and there is evidence of very slight, dorsal blade development. Some photophore groups conform roughly to modern *Polyipnus,* although the fossil supra-abdominal group is more numerous. The cleithrum displays the marked ventral curve typical of the Sternoptychidae and the maurolicid-gonostomatids. There is, however, little flattening of haemal and neural spines. The pelvic girdle, while partially vertical, is still below the rib line, and the body shape, while somewhat broad, is more similar to the maurolicid gonostomatids. There is no spine on the preopercle, the orbit shows no great expansion, and there are no signs of keel plates. This fish, while it has some sternoptychid characters, appears essentially to be maurolicid-gonostomatid. Consequently, its place in the genus *Polyipnus* is questionable, although it may be near the basal stock which gave rise to modern hatchetfishes.

Pauca (1931) described *Sternoptyx prisca* from the lower Oligocene deposits of Piatra Neamţ. The presence of a well-developed dorsal "blade," heavy cleithrum, and pleural rib characteristics place it in the genus *Argyropelecus.* If the dating is correct, it represents the earliest known fossil of this genus.

By Oligocene, and certainly by Miocene times, several examples of the genus *Argyropelecus* were evident in Tethys deposits of Europe (Arambourg, 1929; Daniltshenko, 1960), and in various deposits of California (David, 1943). All of these fossils clearly represent members of the above genus, and *A. logearti* (Arambourg, 1929) appears to be closely related to the modern *A. hemigymnus.*

In the present study, three remarkable fossils from Miocene deposits in California were examined and compared with modern relatives.

Fossil A (Figure 12)

Description. SL 50 mm, body depth 26 mm; dorsal blade from its extension above the dorsal fin origin, low; last pleural rib only slightly reinforced; anterior haemal spines not greatly flattened, postabdominal spines short, symmetrical, not markedly curved; transitional vertebrae two in number; anal pterygiophores relatively simple, not markedly broadened at distal end; anal pterygiophore gap contains two haemal spines; number of anal pterygiophores before gap, seven, after gap, four to five; hypurals 1 and 2 separate; number of vertebrae from posterior margin of dorsal blade to last neural spine, 29.

Fossil B (Figure 13)

Description. Similar to Fossil A above; number of vertebrae from dorsal blade to last neural spine, 30; hypurals 1 and 2 separate; postabdominal spines simple, symmetrical; posteriormost pleural ribs not greatly enlarged.

Fossil C (Figure 14)

Description. SL 60 mm, body depth 40 mm; number of vertebrae from posterior dorsal blade to last neural spine 26, possibly 27; both abdominal and trunk regions greatly broadened; hypurals 1 and 2 fused; anterior haemal spines broad, flat, blade-like; distal end of anal pterygiophores broad, gap well developed, circular, and includes two neural spines.

Fossils A and B are indistinguishable in both key characters and meristics from the modern species *A. affinis* (Fig. 15) and can be assigned to this species complex. Fossil A seems broader than the modern form, but the fossil appears distorted ventrally and there are no other obvious differences.

Fossil C is a member of the *A. lychnus* complex (Figs. 11 and 16). Osteologically there is little difference between *A. olfersi* and *A. lychnus.* However, the fossil has a relatively low dorsal blade, measured from the origin of the dorsal fin rays, a characteristic of *A. lychnus* (Fig. 16). The second transitional vertebra of Fossil C

Figure 12. Fossil A. LACM 1925 (1A), Miocene, Cabrillo Beach, Palo Verdes, California.

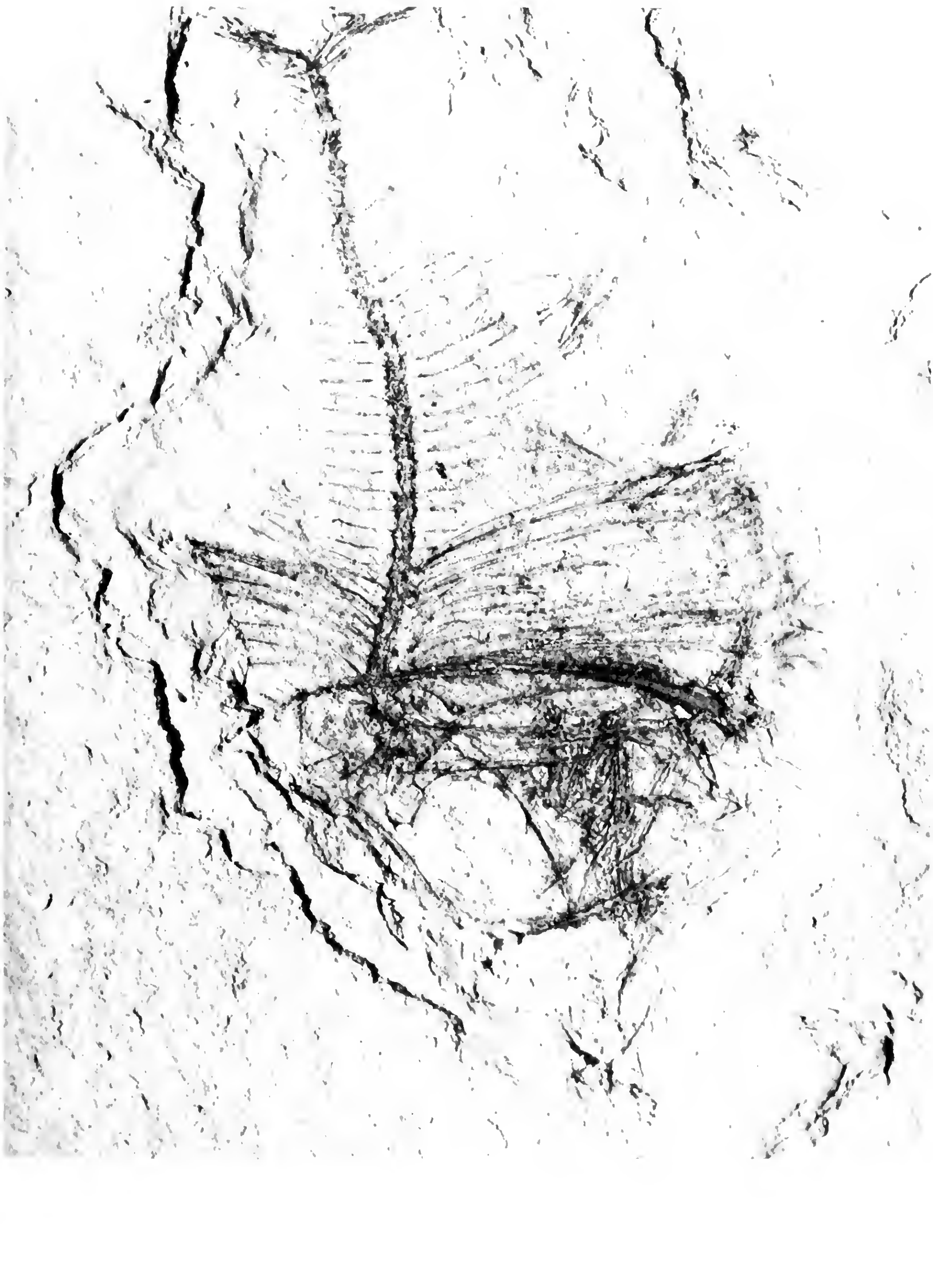


Figure 13. Fossil B. LACM 1925 (6), Miocene, Cabrillo Beach, Palo Verdes, California.

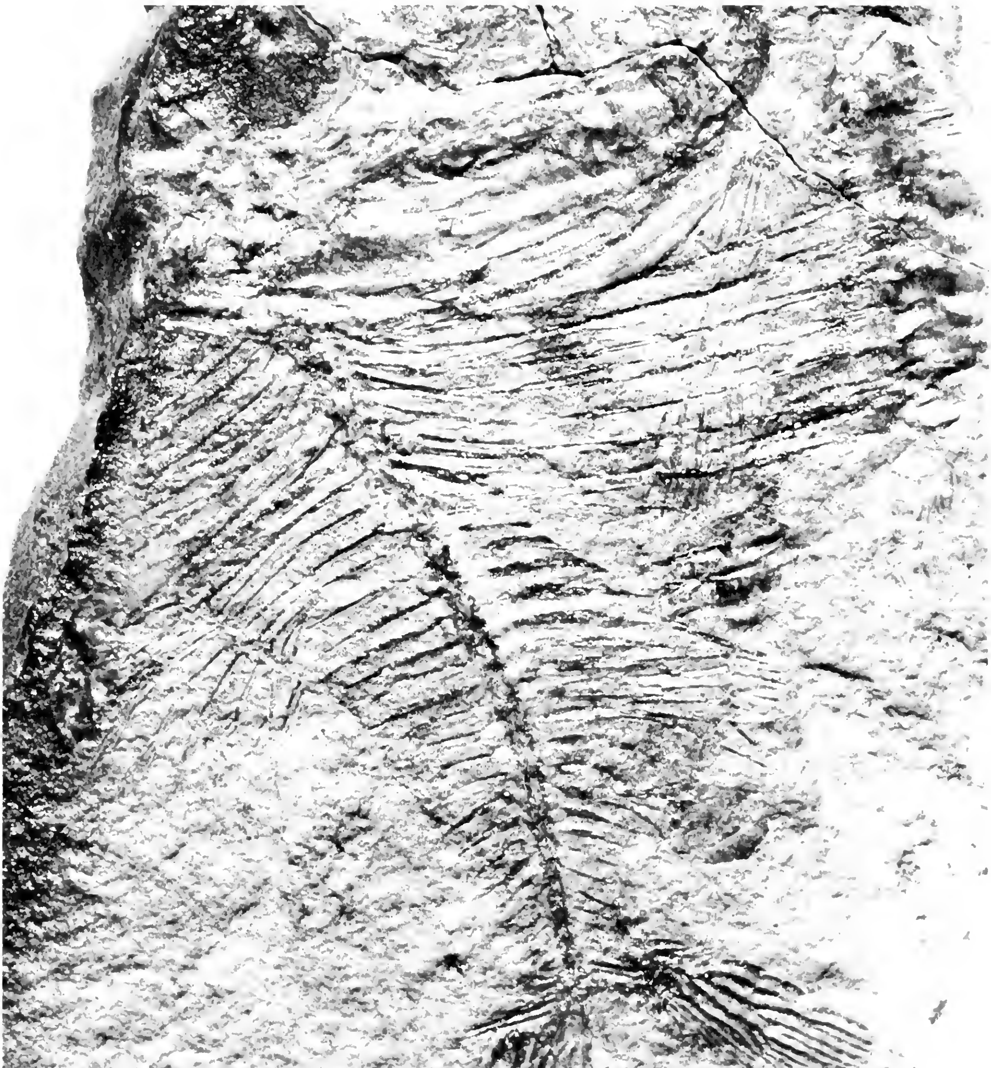


Figure 14. Fossil C. LACM (3), M. Miocene, Bluss Cove, near Malaga, Palo Verdes, California.

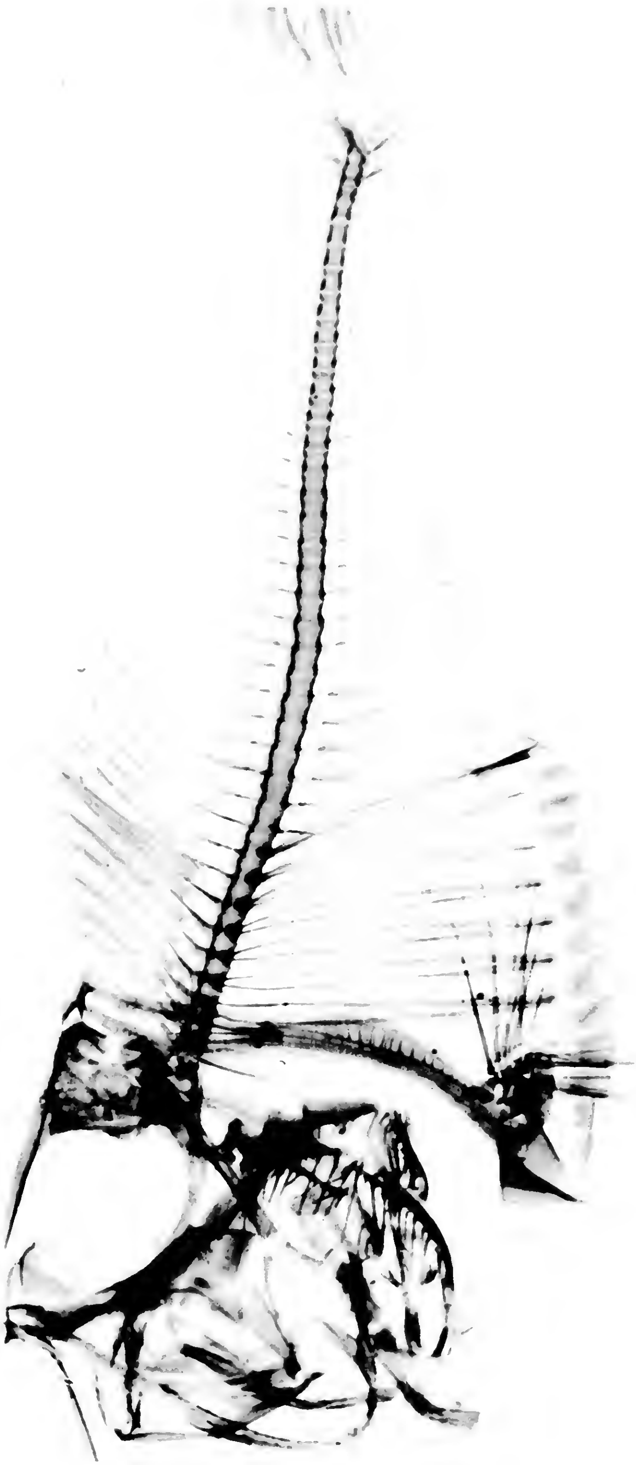


Figure 15. *Argyropelecus affinis:* R/V CHAIN, Cruise 60, RHB 1257; 13° 42′ N; 70° 36′ W.

Figure 16. *Argyrapelecus lychnus*: R/V ANTON BRUUN, Cruise 13, Station 2; 33° 16′ S; 72° 36′ W.

KEY TO THE GENERA OF STERNOPTYCHIDAE

1a. Abdominal photophores 12; telescopic, dorsally oriented eyes; several dorsal pterygiophores form extensive blade anterior to dorsal rays .... genus *Argyropelecus* (p. 31).
b. Abdominal photophores 10; eyes normal; dorsal blade consisting of only one or two spines from a single or two fused pterygiophores 2
2a. Anal photophores 3; no supra-abdominal photophores; single large dorsal spine with anterior serrate extension; first anal pterygiophore greatly enlarged, supporting triangulate transparent membrane above anal fin rays .... genus *Sternoptyx* (p. 67).
b. Anal photophores 6 or greater; 3 supra-abdominal and a lateral photophore; dorsal blade reduced; no large transparent membrane above anal fin rays .... genus *Polyipnus* (p. 79).

has a pair of vestigial ribs whereas the one modern *A. lychnus* examined does not. One of the specimens of *A. olfersi* examined has small vestigial ribs on this vertebra; otherwise, all of the fossil characters and vertebral counts are identical to these modern species. Fossil C is probably *A. lychnus* or at least its immediate predecessor.

By mid-Miocene times evolution within the genus *Argyropelecus* was essentially complete and species distributions show modern characteristics. This genus with its many specializations must have originated by the late Eocene at the latest and possibly as far back as the Paleocene or late Cretaceous.

During or prior to the early Cretaceous, some members of the early salmonoid fishes began to adapt to a deep water environment. After the basic adaptations to this environment were acquired (at latest mid-to-late Cretaceous) there was considerable stomiatoid radiation which continued into the late Eocene to early Oligocene. This radiation led to many diverse forms, of which the maurolicid-gonostomatids were one. Within the latter, an ancestor, possibly resembling *P. sobniowiensis,* gave rise to a form or series of forms with many features of the modern genus *Polyipnus.* From this basic stock the modern genera evolved, conceivably quite rapidly. By the Miocene, evolution was practically complete in the specialized *Argyropelecus* and possibly the other genera as well. The stomiatoid-gonostomatid radiations of the early tertiary show evidence of being fairly complete by that time also. Many modern gonostomatid genera were present during that time, and Miocene faunas have distinctly modern resemblances (David, 1943; Grey, 1964; Crane, 1966; Daniltshenko, 1960). The salmonoid-derived midwater fauna appears to have replaced earlier forms during the early Tertiary, and it remains the dominant element today.

SYSTEMATICS

Family STERNOPTYCHIDAE

Type Genus: *Sternoptyx* Hermann 1781

Diagnosis. Neural spine of first preterminal vertebra vertically oriented, broadened, with triangulate paddle shape, no fin rays attached; second preterminal vertebra modified for support of first (except *P. spinosus* complex); basipterygia vertically oriented, spine bearing, contained dorsally within, and closely joined to the ventral margin of the posterior pleural ribs; pelvic fin rays vertically oriented; six to seven pleural ribs enlarged to form an expanded rib cage; epiotics meet below supraoccipital; parietals well developed, bearing dorsolateral ridges; one or more dorsal pterygiophores enlarged to form blade or spinelike extension anterior to dorsal rays; anal pterygiophores form characteristic gap below anal photophore group; preopercle bearing well-developed ventral spine.

Description. Bright silvery colored, small fishes; standard length usually less than 90 mm; body deep, strongly compressed; bony scalelike plates form keel below ventral photophore groups (except

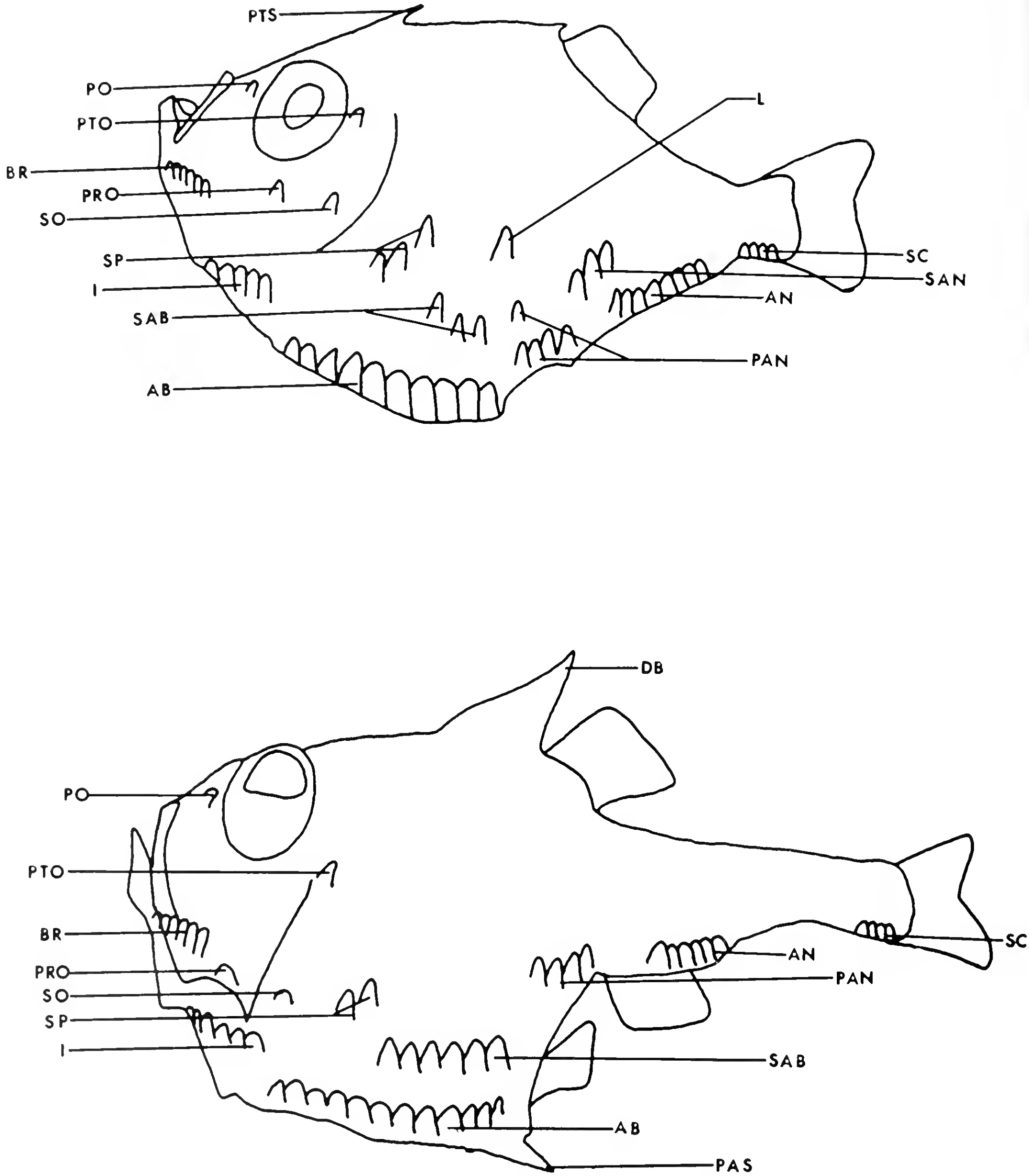


Figure 17. Photophore and spine characteristics: top—*Polyipnus*; bottom—*Argyropelecus*. Abbreviations—photophores: see p. 6; spines: DB = dorsal blade; PAS = postabdominal spine; PTS = post-temporal spine.

Sternoptyx); 10–12 abdominal, and four subcaudal photophores always present (see Figs. 17 and 18 for photophore and spine characteristics); nasal lamallae well developed; digestive tract simple, with thick muscular stomach, five or more plyroic caecae, and short straight intestine; eyes large, well developed; gape vertical; adipose fin usually present; scales thin or absent except along ventral surface; swim

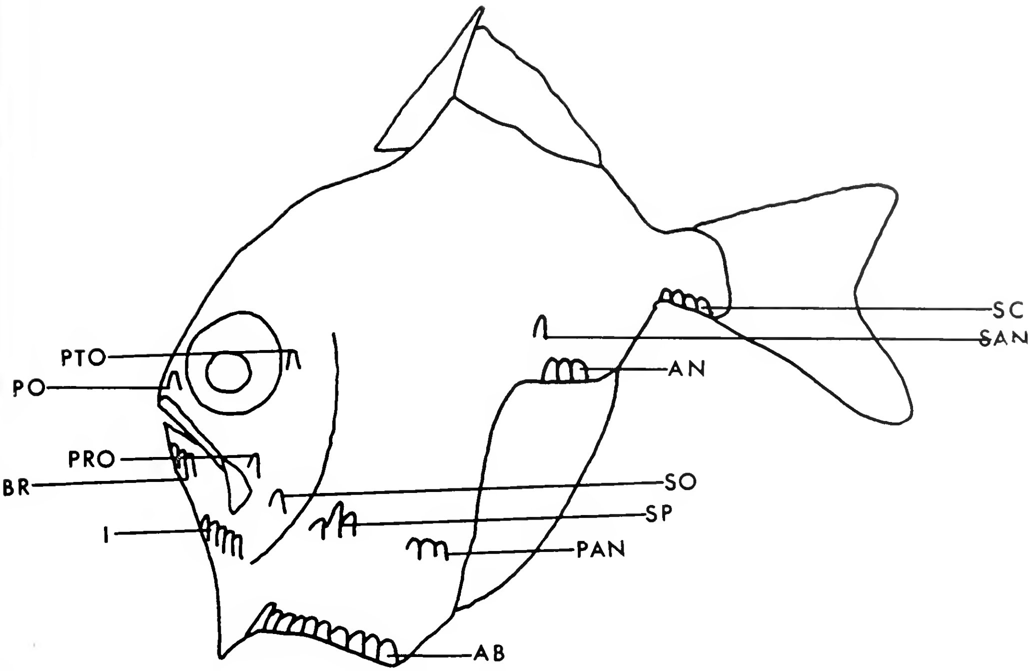


Figure 18. Photophore characteristics: genus *Sternoptyx*. Abbreviations: see p. 6.

bladder present (see above for osteological description).

Genus *Argyropelecus* Cocco, 1829

Argyropelecus Cocco, 1829: 146 (type species: *Argyropelecus hemigymnus* Cocco, 1829, by monotypy).

Pleurothysis Lowe, 1843: 64 (type species: *Sternoptyx olfersi* Cuvier, 1843, by original designation).

Sternoptychides Ogilby, 1888: 1313 (type species: *Sternoptychides amabilis* Ogilby, 1888, by monotypy).

Diagnosis. Twelve abdominal, six supra-abdominal and two suprapectoral photophores; eyes telescopic, dorsally oriented; frontal ridges compressed dorsally above eyes; basisphenoid absent; several teeth directed anteriorly on posterior maxillary margin; dorsal "blade" consisting of several broadened pterygiophores anterior to dorsal rays; seven enlarged pleural ribs.

Description. Photophores: PO 1; PTO 1; BR 6; I 6; AB 12; PRO 1; SO 1; SP 2; SAB 6; PAN 4; AN 6; SC 4 (for anatomical details see Brauer, 1908; Bassot, 1966).

Spines: Post-temporals extended posteriorly to form a small spine; preopercle bears one ventrally and one posteriorly directed spine; retroarticular bears ventrally directed spine; basipterygia extended ventrally bearing one or two postabdominal spines; cleithrum extends ventrally forming preabdominal spine; spiny scales present in adults of some species below subcaudal and preanal photophores.

Eyes: Large, well developed, telescopic, lens dorsally oriented, fitting into dorsal grooves in the frontal bone.

Gill Rakers: Total 15–24; rakers well developed with rough toothlike surface; epi- and ceratobranchials bear well-developed spines on internal surface.

Jaws and Dentition: Jaws somewhat vertically oriented; premaxilla well developed, toothed, and major upper jaw bone in gape; maxilla also somewhat in-

cluded in gape, toothed, the posteriormost teeth curved markedly forward; lower jaw sturdy, heavily toothed, occasionally with large canines; dentition consisting of multi-rowed single cusped, curved caninelike teeth; palatine teeth present, often well developed; epibranchial of third and fourth arch extends ventrally and laterally to form toothed plates.

Meristics: Vertebrae 35–40; C. 9+10; D. 8–10; A. 6–8 + 5–6.

Color: Bright silvery in life, quickly lost in formalin preservative; dark pigmentation often striated posteriorly; stable for long periods in preservation.

Internal Anatomy: Relatively thin-walled swim bladder (see Marshall, 1960) and gas gland well developed; digestive tract simple, consisting of heavily pigmented, double compartmented stomach; the anterior internal lining very thick walled and covered with rasping tubercles; posterior lining thin and distensible, five to seven thick-fingered pyloric caecae, large liver, and a short straight intestine; caelomic cavity lined with heavily pigmented membrane; gonads when mature fill the dorsal and lateral posterior half of the body cavity; nephritic tissue moderately well developed.

Species complexes. There has been substantial radiation within the genus and even to some extent within the species complexes. The *A. affinis* complex appears to be the most primitive and other forms can be derived from it. Primitive characters of this complex include: three hypural elements in lower caudal lobe; posterior ventral photophores in an almost unbroken series; glandular photophore arrangement simple, the posterior photophores not joined in glandular clusters; little reinforcement of posteriormost pleural rib; body not markedly deepened anteriorly; basipterygia lacking support arm for keel plates; generally unspecialized axial skeleton, including lack of marked broadening of anterior haemal spines; vertebral number 38–40.

The more advanced members of the genus are characterized by two hypural elements in the lower caudal lobe; posterior photophores joined into distinct glandular clusters; a general deepening of the anterior body region with subsequent reduction in vertebral number; increased complexity of structural ossification especially in the axial skeleton, including a marked reinforcement of the last large pleural rib, and a keel supporting extension on the left basipterygia.

A. hemigymnus appears slightly more primitive than the *A. lychnus* complex and is highly specialized. Important characters include: primitive transitional vertebrae (like *A. affinis*); dwarfism (maximum length 38–40 mm); fused basipterygia forming single postabdominal spine; 38 vertebrae; epiotics with dorsal extensions (Fig. 7); peculiar dorsal blade shape, often with supplementary spiny spurs on the major element.

The most specious group, the *A. lychnus* complex, shows a high degree of structural ossification in the axial skeleton, including the dorsal and anal pterygiophore systems; some species have developed long, fang-like canines in the lower jaw; there is a marked deepening of the anterior body region with reduction in vertebral number.

Key to the Species of *Argyropelecus*

1a. Supra-abdominal, preanal, anal, and subcaudal photophores in a nearly continuous straight line; subcaudal photophores separate, an appreciable gap between each photophore; 3 separate hypural elements in lower caudal lobe ...... *A. affinis* complex 3

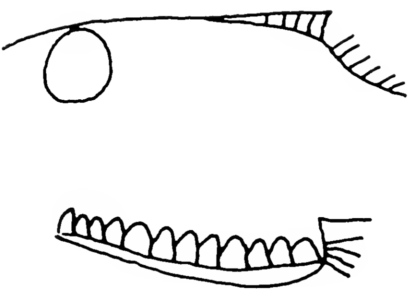
b. Supra-abdominal, preanal, anal, and subcaudal photophores not in a continuous straight line; subcaudal photophore group in a single glandular cluster, no appreciable gap between each photophore; two separate hypural elements in lower caudal lobe 2

2a. A single posteriorly directed, serrate postabdominal spine; gap between anal and subcaudal photophore groups greater than 2.2 times gap between preanal and anal groups; dorsal rays 8 ...... *A. hemigymnus* (p. 42).

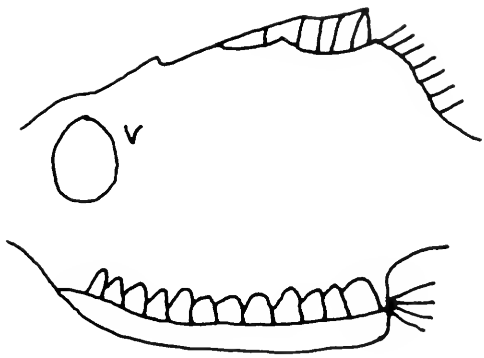
b. Two separate postabdominal spines; anal subcaudal gap less than 2.0 times anal–preanal gap; dorsal rays 9 .... *A. lychnus* complex 4

3a. Dorsal blade low, its height less than one-third its length; body margin not markedly raised posterior to dorsal blade; ventral keel scales do not extend far below abdominal photophores; no laterally directed sphenotic spine near dorsal, posterior edge of orbit .... *A. affinis* (p. 34).

b. Dorsal blade high, its height greater than one-third its length; body margin markedly raised posterior to dorsal blade; ventral keel scales extend well below abdominal photophores forming flaplike process; prominent laterally directed sphenotic spine near dorsal, posterior edge of orbit .... *A. gigas* (p. 38).



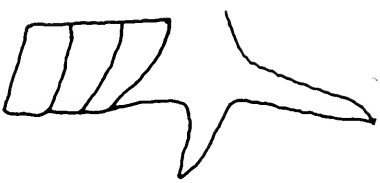
a.



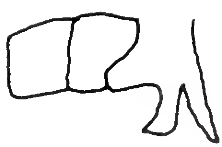
b.

4a. Posterior postabdominal spine directed posterioventrally and markedly larger than the anterior; anterior margin of posteriormost abdominal keel scale slants markedly forward; standard length less than 3.4 times body depth; pair of enlarged canine teeth present in lower jaw; subcaudal spines present .... *A. aculeatus* (p. 48).

b. Both postabdominal spines of about equal length and size; anterior margin of posteriormost abdominal keel scale almost vertical; SL greater than 3.5 times body depth; pair of enlarged canines may or may not be present in lower jaw; subcaudal spines may or may not be present 5



a.



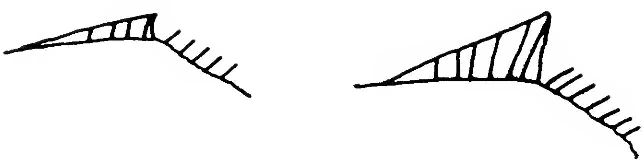
b.

5a. Pair of enlarged canine teeth in lower jaw; sharply pointed anteriormost postabdominal spine curved markedly and evenly forward; upper preopercular spine short, not extending much beyond posterior border of preopercle; outermost tips of dorsal and ventralmost caudal rays streaked with dark pigment (fish greater than 35 mm) .... *A. olfersi* (p. 52).

b. No pair of enlarged canines in lower jaw; anteriormost postabdominal spine squared or blunt (except very small individuals), not curving evenly forward; upper preopercular spine extends well beyond posterior border of preopercle; no pigment on outermost caudal rays 6

a. b.

6a. Dorsal blade low, blade height less than 2.5 mm for SL 25–50 mm, less than 3.1 mm for SL 50–70 mm; body narrow (see regression, body depth, Table 11); no spines on scales below subcaudal photophores; dark well-developed pigment spots form line along posterior midline (especially in smaller sizes); upper preopercle spine usually curved dorsally, never ventrally .... *A. sladeni* (p. 56).
b. Dorsal blade high, blade height greater than 2.7 mm for SL 25–50 mm, greater than 3.8 mm for SL greater than 50 mm; body robust (see regression, body depth, Table 14); spiny scales present below subcaudal photophores (fish greater than 30 mm SL); pigment spots minute along posterior midline; upper preopercle spine usually curved ventrally, never dorsally .... *A. lychnus* (p. 63).



a. b.

Argyropelecus affinis Garman
Figure 19

Argyropelecus affinis Garman, 1899: 237 (holotype USNM 44593; tropical North Atlantic; not seen); Brauer, 1901: 120; 1906: 103 (fig. larvae); Regan, 1908: 218; Barnard, 1925: 153; Norman, 1930: 301 (fig.); Jespersen, 1934: 15 (fig.); Fowler, 1936: 221; Beebe, 1937: 201; Parr, 1937: 49; Norman, 1939: 19; Nybelin, 1948: 23; Misra, 1952: 367; Smith, 1953: 102; Haig, 1955: 321; Fowler, 1956: 67; Schultz, 1961: 597 (fig.); Bahamonde, 1963: 83; Blache, 1964: 71 (fig.); Schultz, 1964: 241 (fig.); Backus et al., 1965: 142; Bussing, 1965: 185; Bright and Paquegnat, 1969: 27.

Argyropelecus pacificus Schultz, 1961: 599 (fig.); 1964: 241; Berry and Perkins, 1965: 625; Lavenberg and Ebeling, 1967: 185.

Species distinction. Differs from *A. gigas* (in addition to key characters) by its narrower body depth and trunk (see regression, body depth, Tables 2 and 3); less distinct trunk striations; relatively longer teeth in lower jaw; less well-developed post-temporal spines; smooth dorsal body surface; and less well-developed neurocranial crests (frontals, sphenotics, and parietals).

Description. D. 9; A. 12–13; P. (10) 11; total gill rakers 18–22; vertebrae 38–39 (40).

Medium size species rarely exceeding 70 mm SL; body more evenly tapered than others in genus; body depth at end of dorsal greater than 3.5 times into SL; caudal peduncle long and narrow, its depth

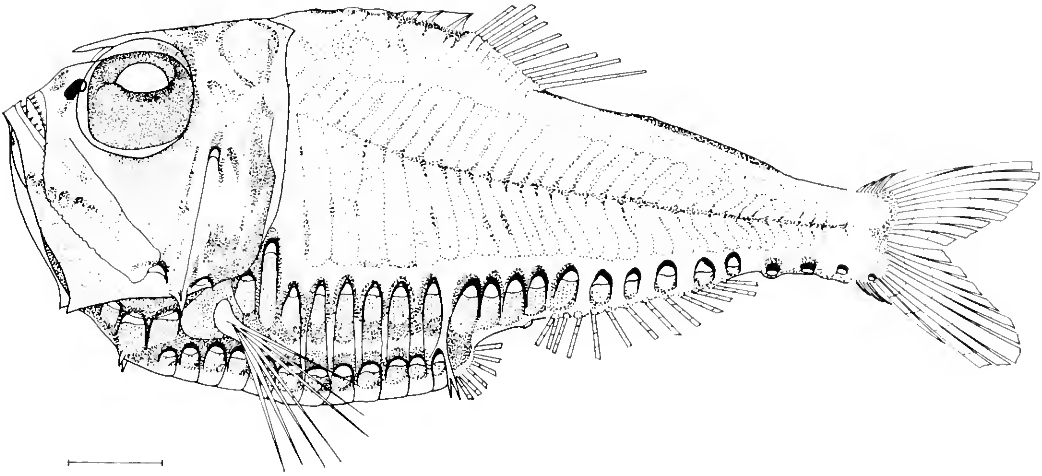


Figure 19. *Argyropelecus affinis;* R/V CHAIN, Cruise 60; Station 1257; SL 51 mm.

less than length of subcaudal photophore group; dorsal spine low, its height less than one-third its length; post-temporal spine short; postabdominal spines of equal size, with no marked curving; dorsal preopercle spine directed latero-anteriorly; ventral preopercle spine long, curved anteriorly; jaws large; teeth short, recurved, better developed in lower jaw; gill rakers long, closely set; in preservative, trunk

TABLE 2. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. AFFINIS*.

Character	Regression A	Regression B
Indian Ocean (5°–12°N, 160°–168°E)		
Body depth	–1.83	0.49 ± .146
Jaw length	–0.78	0.25 ± .065
		N = 11
Gulf of Guinea		
Body depth	–2.44	0.46 ± .121
Jaw length	–0.27	0.22 ± .060
Jaw width	–0.23	0.12 ± .059
		N = 10
NW Atlantic (30°–33°N, 73°–78°W)		
Body depth	2.59	0.37 ± .176
Jaw length	–0.78	0.24 ± .107
Jaw width	–1.35	0.14 ± .087
		N = 7
SE Pacific (Chile)		
Body depth	0.55	0.42 ± .086
Jaw length	0.64	0.21 ± .047
		N = 13
NE Pacific (California)		
Body depth	–1.02	0.49 ± .062
Jaw length	0.27	0.22 ± .029
		N = 19

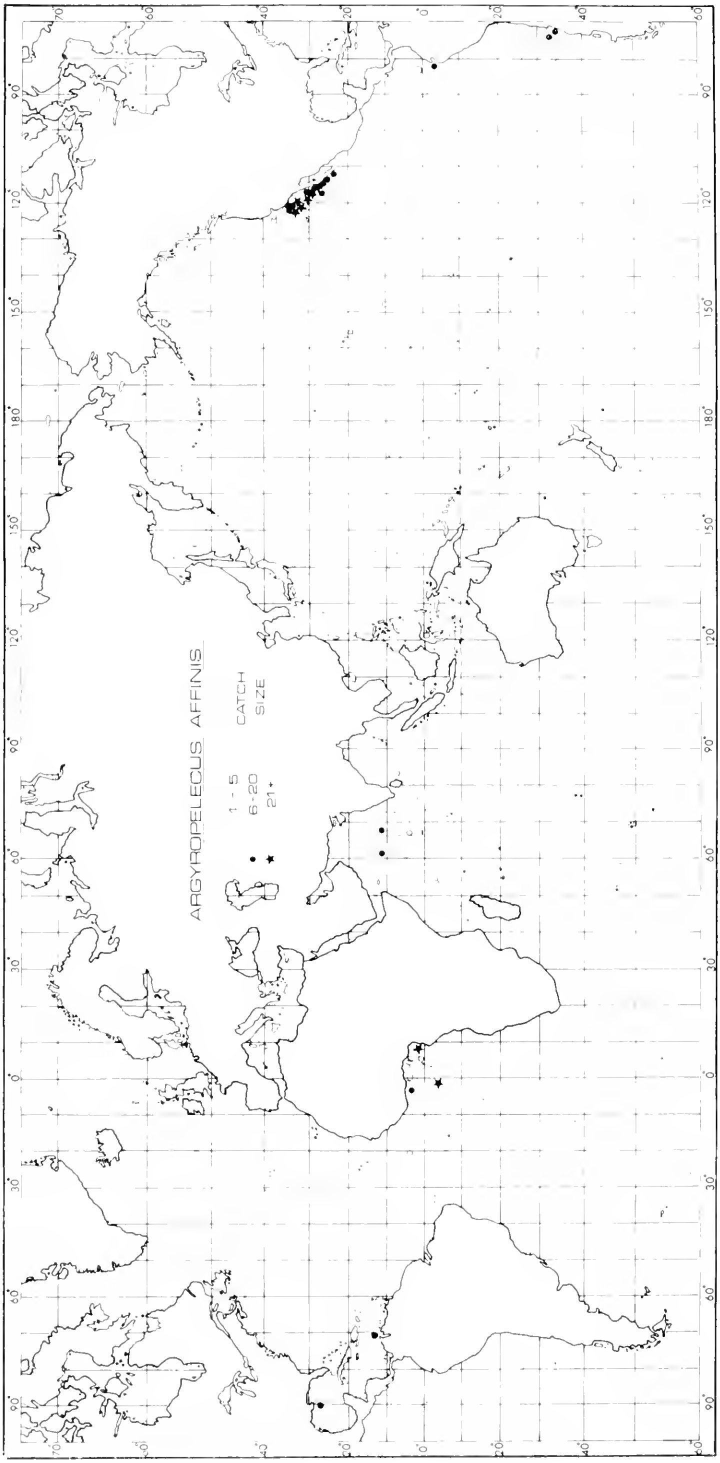


Figure 20. Horizontal distribution of *A. affinis*. Catch size categories refer to the number of individuals taken in that haul.

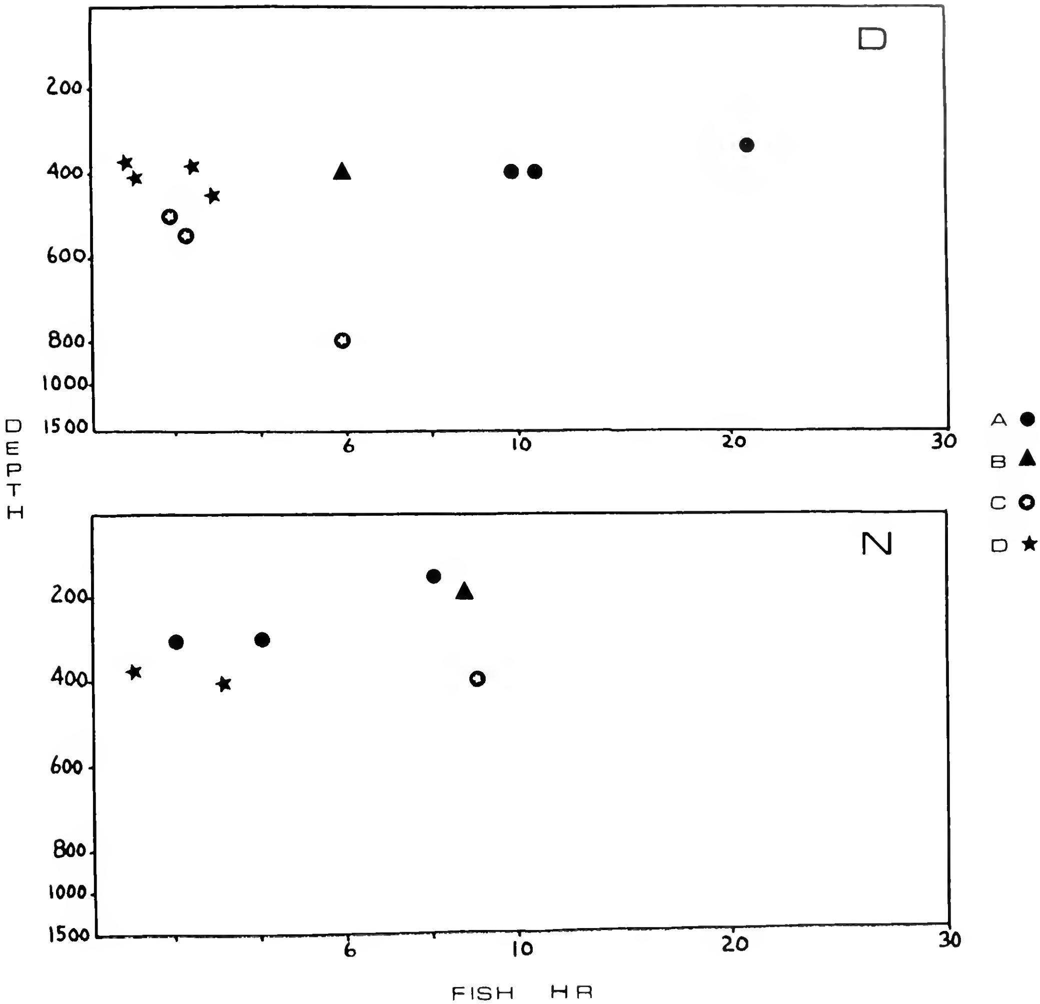


Figure 21. Diurnal vertical distribution of *A. affinis* determined by rate of capture with depth during the day (D) and night (N). A = Pacific (California); B = Pacific (Chile); C = Gulf of Guinea; D = Gulf of Mexico and Caribbean.

region exhibits cross pigment striations with well-defined, midlateral line.

Distribution. Horizontal distribution (Fig. 20): Taken abundantly in the Gulf of Guinea, off California, Chile, and in the northern Indian Ocean; moderate catches are recorded from the northern Gulf of Mexico and the coast of Venezuela in the Caribbean; smaller catches which may represent possible populations are recorded southeast of Hawaii, south of Java, and off the southeast coast of the United States; scattered samples representing this species appear in the Bay of Bengal, Gulf of Aden, tropical Atlantic, and off the southeast coast of Brazil. (Additional records: Atlantic, occasional catches between Azores and Madeira; Pacific, moderate catches near coast of northern Peru.)

Vertical distribution (Fig. 21): Appears concentrated between 350 m and 600 m by day with the highest concentrations in the vicinity of 400 m; by night the distribution is somewhat more shallow, major

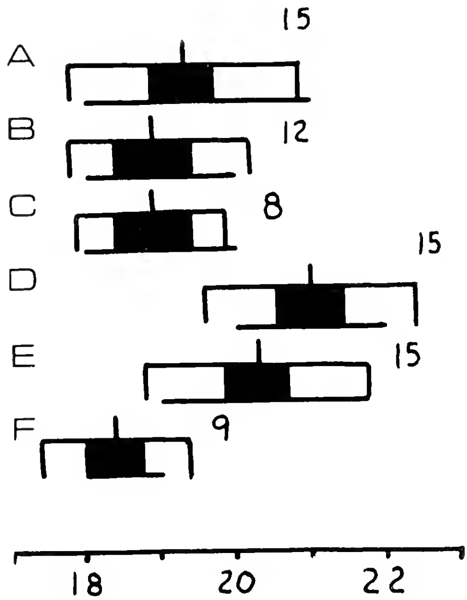


Figure 22. Geographic variation in gill raker number in *A. affinis*. A = Gulf of Guinea; B = Caribbean; C = Indian Ocean; D = Pacific (Chile); E = Pacific (California); F = NW Atlantic (NW Atlantic pocket). Numbers refer to sample size.

concentrations occurring from 170 m to 400 m. With the possible exception of the Gulf of Guinea, there are no indications of marked geographic variation in depth distribution, although Appendix C indicates slightly shallower daytime depths off California than in the tropical Atlantic.

Geographic variation. Five separate populations could be recognized and are identified and statistically defined in Figures 22 and 23 and Table 2. Regression sample sizes are small in the Atlantic. Figure 23 indicates positional variation in body depth even though there is no significant difference in slope.

Argyropelecus gigas Norman
Figure 24

Argyropelecus gigas Norman, 1930: 302 (holotype BMNH 1.12.329; Gulf of Guinea; not seen); Jespersen, 1934: 15 (fig.); Fowler, 1936: 1208; Parr, 1937: 49; Maul, 1949a: 17 (fig.); 1949b: 13; Koefoed, 1961: 3; Schultz, 1961: 600 (fig.); 1964: 241 (fig.); Blache, 1964: 71 (fig.); Backus et al., 1965: 129; Bright and Paquegnat, 1969: 28.

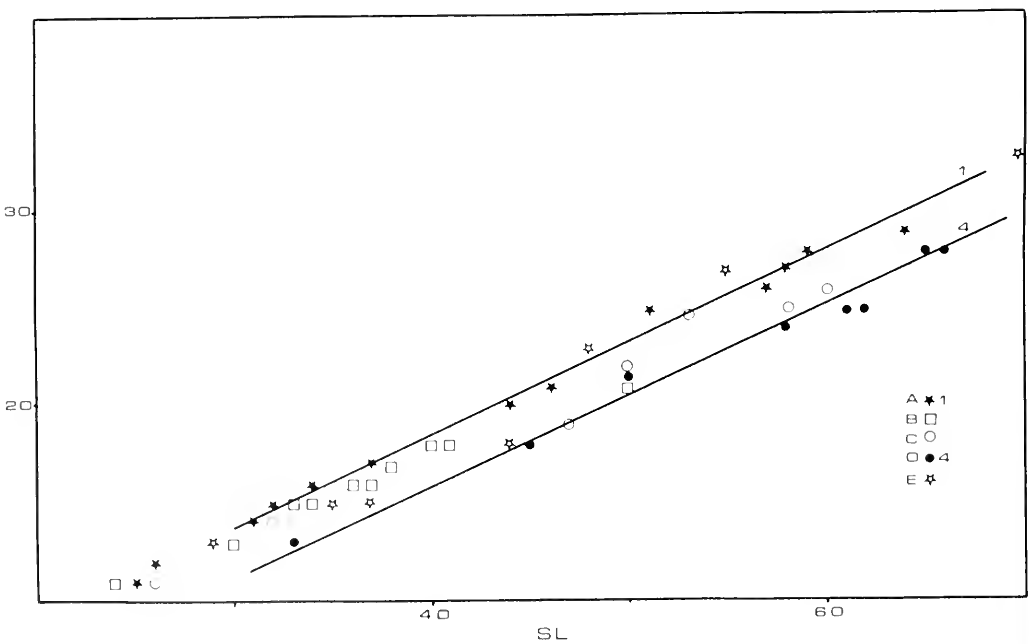


Figure 23. Geographic variation in the regression of body depth (BD) on standard length (SL) in *A. affinis*. A = Pacific (California); B = Pacific (Chile); C = NW Atlantic; D = Gulf of Guinea; E = Indian Ocean.

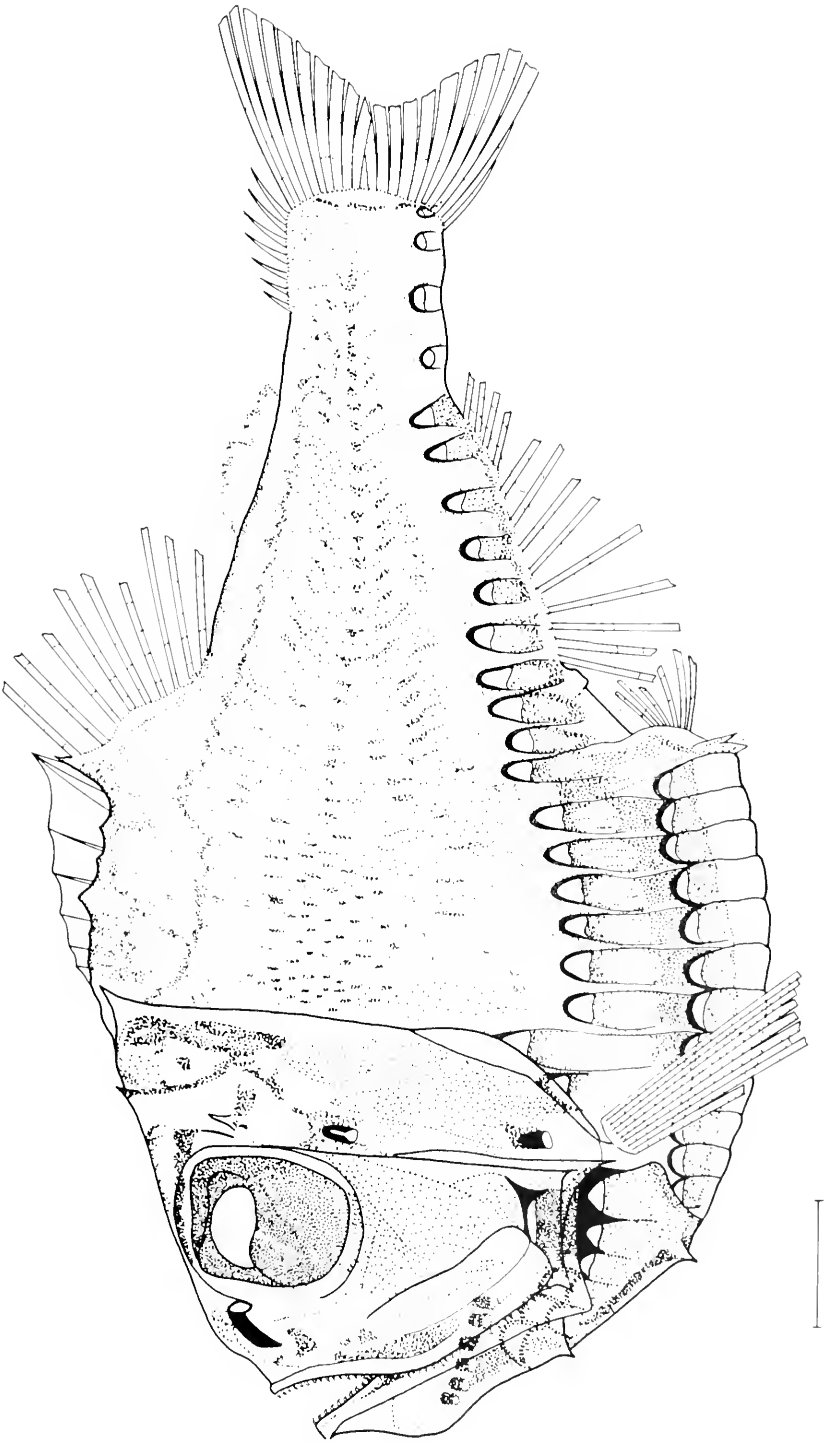


Figure 24. *Argyropelecus gigas*; R/V CHAIN, Cruise 60; Station 1308; SL 52 mm.

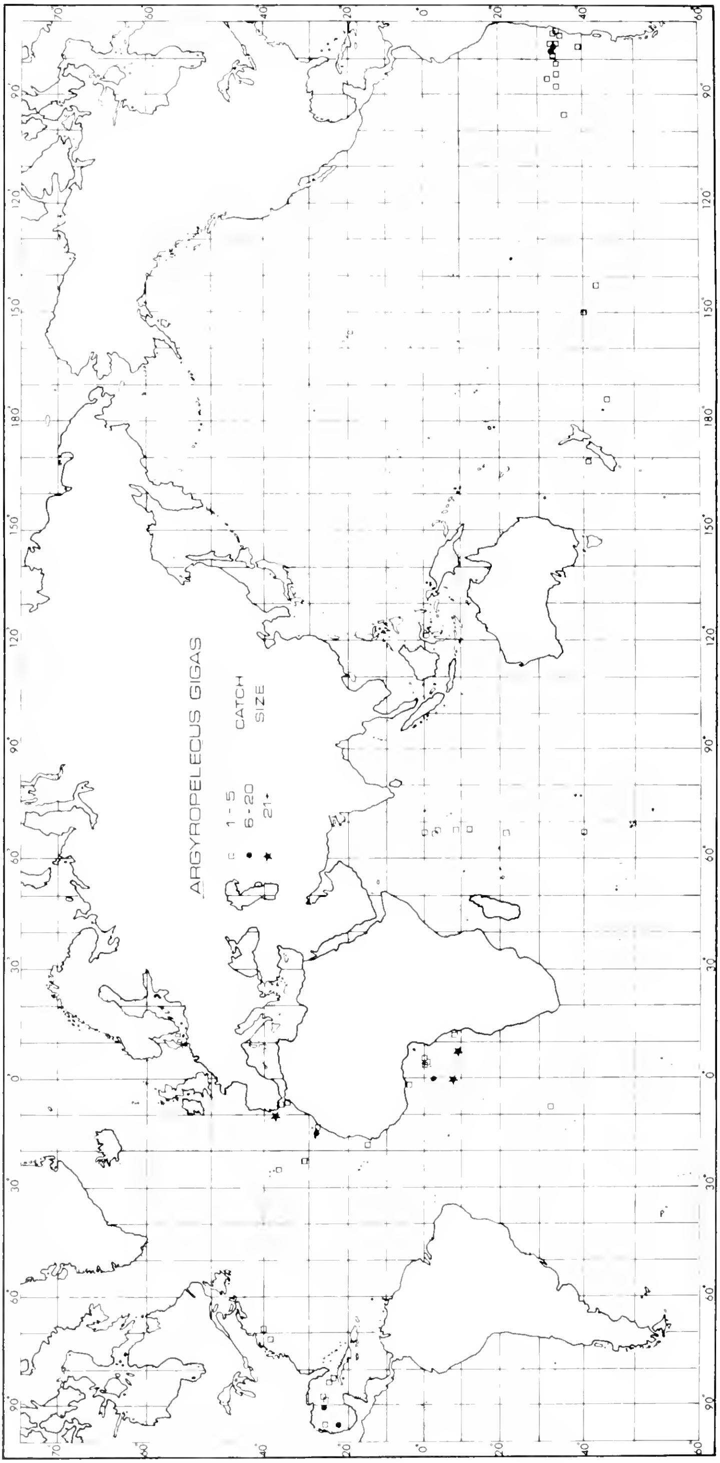


Figure 25. Horizontal distribution of A. *gigas*. Catch size categories refer to the number of individuals taken in that haul.

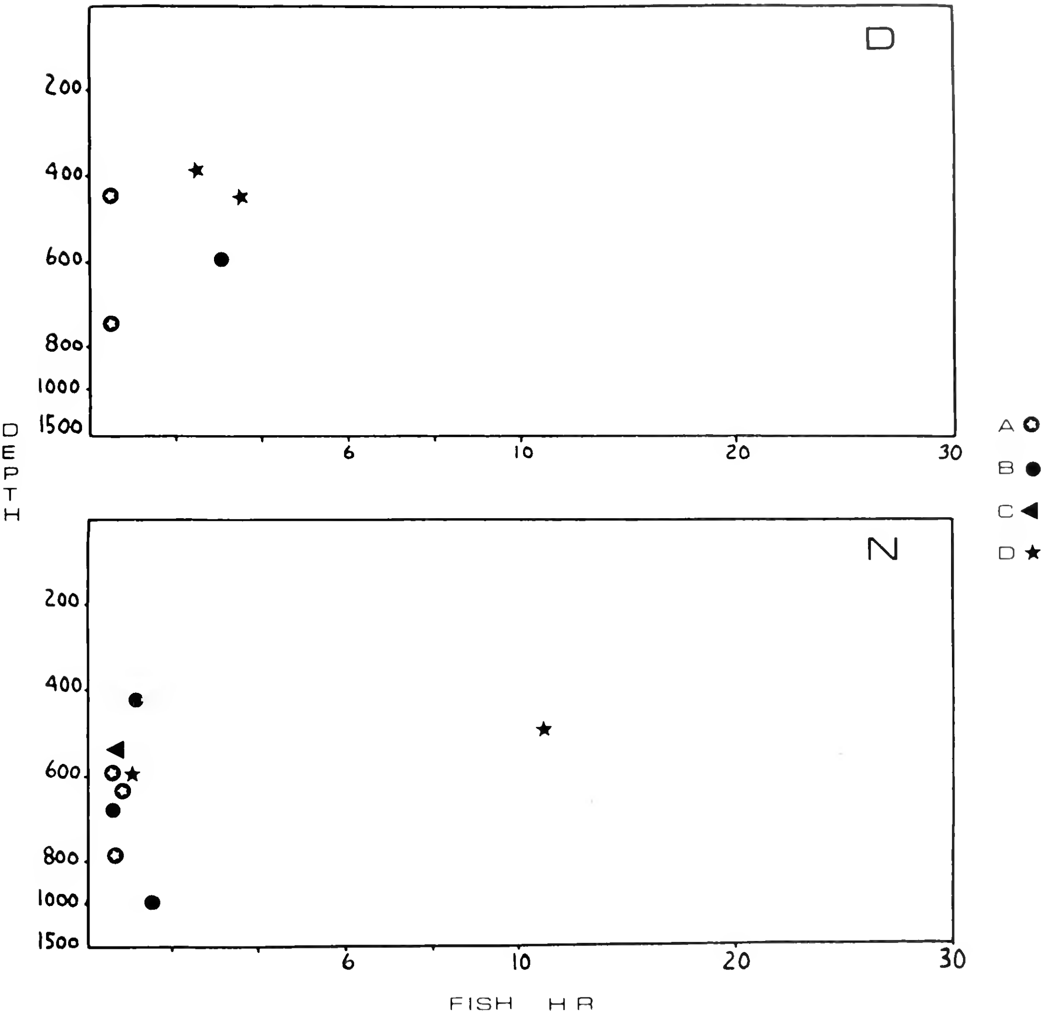


Figure 26. Diurnal vertical distribution of *A. gigas* determined by rate of capture with depth during the day (D) and night (N). A = Pacific (Chile); B = Gulf of Guinea; C = Gulf of Mexica; D = NE Atlantic.

Argyropelecus affinis: Jespersen, 1915: 6; Roule and Angel, 1933: 46; Buen, 1935: 52; Nybelin, 1948: 23; Dollfus, 1955: 1.

Species distinction. See *A. affinis* (p. 34).

Description. D. 9 (10); A. 12–13; P. 10–11; total gill rakers 18–21; vertebrae 38–39.

Giant species often exceeding 110 mm SL; trunk triangulate, body depth at end of dorsal less than 3.3 times into SL; caudal peduncle deep, its depth nearly equal to subcaudal photophore length; dorsal spine high, its height greater than one-third its length; post-temporal spine prominent; postabdominal spines symmetrical; preopercle spines as in *A. affinis;* jaws large; teeth small, recurved, a pair of larger canine teeth in upper jaw (premaxilla); gill rakers well developed; parietals, post-temporal, frontals and sphenotics with prominent spines or flanges; in preserva-

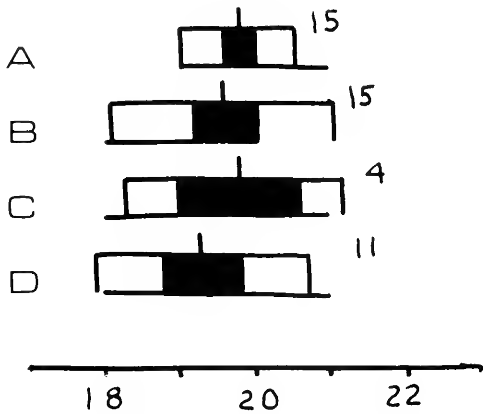


Figure 27. Geographic variation in gill raker number in *A. gigas*. A = NE Atlantic; B = Gulf of Guinea; C = Indian Ocean; D = Pacific (Chile). Numbers refer to sample size.

tive pigment in small spots along midline; very heavy mucoid secretion often present.

Distribution. Horizontal distribution (Fig. 25): Although occurring in all oceans except the North Pacific, this species appears quite restricted locally. It is taken in abundance in the Gulf of Guinea, in the eastern North Atlantic off North Africa and southern Spain, in the northern Gulf of Mexico, and off Chile in the South Pacific; small catches of this species are recorded along longitude 67°E from the equator to 40°S in the Indian Ocean, across the South Pacific between 35°S and 50°S from Chile to New Zealand in the South Pacific, and between New York and Cape Cod in the North Atlantic. Additional records: 36°35′S, 95°28′E.

Vertical distribution (Fig. 26): Concentrated between 400 m and 600 m; no indication of diurnal vertical movement or marked geographic variation in depth distribution.

Geographic variation. While having the most disjunct horizontal distribution in the family, this species shows the least variability in the characters measured (Fig. 27, Table 3). Sample sizes in most cases were quite small, and increased sampling and the use of other characters may result in better population definition.

Argyropelecus hemigymnus Cocco
Figure 28

Argyropelecus hemigymnus Cocco, 1829: 146 (holotype unknown; Mediterranean, Messina); Alcock, 1896: 331; Jordan and Evermann, 1896:

TABLE 3. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. GIGAS*.

Character	Regression A	Regression B
Gulf of Guinea		
Body depth	0.65	0.50 ± .131
Jaw length	0.71	0.21 ± .055
Jaw width	−0.33	0.14 ± .040
		N = 10
NE Atlantic (37°N, 10°W)		
Body depth	−4.42	0.58 ± .104
Jaw length	0.23	0.22 ± .044
Jaw width	−1.36	0.16 ± .029
		N = 14
Indian Ocean (0°–40°S, 167°E)		
Body depth	−0.60	0.54 ± .332
Jaw length	0.39	0.22 ± .137
		N = 5
SE Pacific (Chile)		
Body depth	−2.21	0.54 ± .155
Jaw length	−0.71	0.24 ± .068
		N = 9

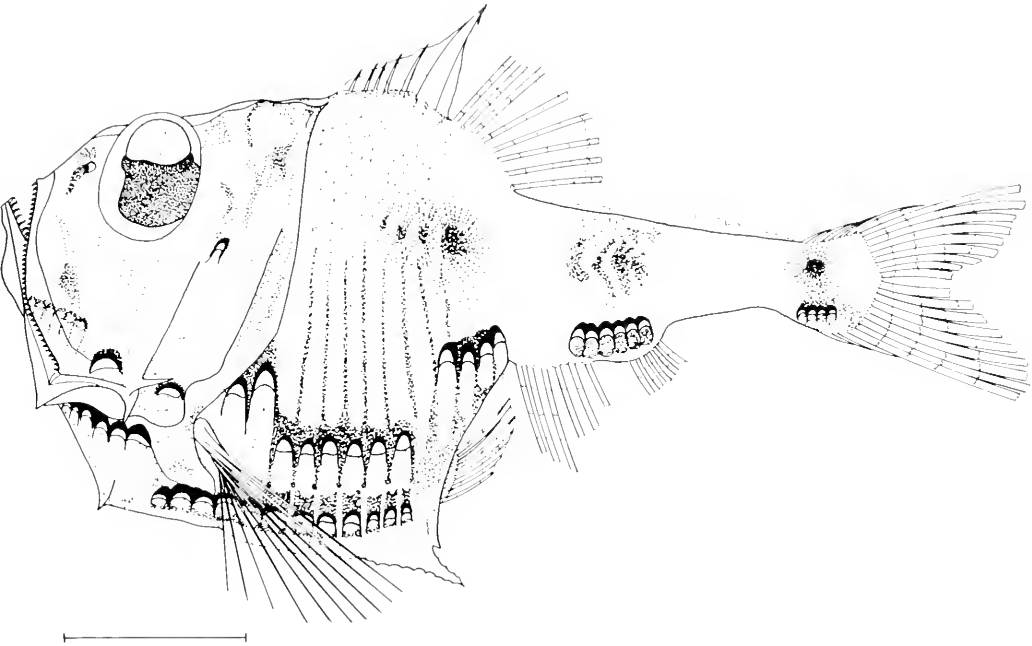


Figure 28. *Argyropelecus hemigymnus*; R/V CHAIN, Cruise 60; Station 1299; SL 30 mm.

604; Handrick, 1901: 1 (anatomy, nervous system, light organs); Collett, 1903: 108; Ledenfeld, 1905: 170 (light organs); Brauer, 1906: 106 (larvae, fig.); Regan, 1908: 218; Ehrenbaum, 1909: 357 (larvae, fig.); Zugmayer, 1911: 52; Holt and Byrne, 1913: 21 (larvae, fig.); Jespersen, 1915: 6; Jespersen and Tåning, 1919: 220 (larvae, eye muscles); Nusbaum-Hilarowicz, 1923: 10 (anatomy); Barnard, 1925: 153; Jespersen and Tåning, 1926: 59; Sanzo, 1928: 50 (eggs, larvae). Norman, 1930: 301; Borodin, 1931: 44 (eggs, larvae); Jespersen, 1934: 15 (larvae, fig.); Buen, 1935: 52; Fowler, 1936: 1208; Beebe, 1937: 201; Parr, 1937: 49 (spines); Norman, 1937: 82; 1939: 19; Nybelin, 1948: 23; Maul, 1949b: 13; Misra, 1952: 367; Smith, 1953: 102; Kotthaus and Krefft, 1957: 3; Perès, 1958: 4 (bathyscaphe); Koefoed, 1961: 5; Schultz, 1961: 601; 1964: 241; Blache, 1964: 71; Backus et al., 1965: 139; Kotthaus, 1967: 22 (photo, otoliths); Bright and Paquegnat, 1969: 28.

Argyropelecus d'urvilli Valenciennes, *in* Cuvier and Valenciennes, 1849: 405; Goode and Bean, 1896: 127.

Argyropelecus intermedius Clarke, 1878: 245; Schultz, 1961: 587; 1964: 241; Blache, 1964: 71; Berry and Perkins, 1965: 625; Kotthaus, 1967: 11 (photo.); Lavenberg and Ebeling, 1967: 185.

Argyropelecus heathi Gilbert, 1905: 601; Fowler, 1949: 42; Haig, 1955: 321.

Species distinction. Differs from all other species in genus by its narrow trunk, single postabdominal spine, small size, minute teeth, presence of only eight dorsal and eleven anal rays.

Description. D. 8; A. 11; P. 10–11; total gill rakers (18) 19–23 (24); vertebrae (36) 37–38.

Dwarf species rarely exceeding 38 mm SL; trunk very long and narrow; its depth at origin of anal photophores three or more times into greatest body depth, subcaudal photophores well separated from anals; dorsal spine medium-to-high, its height often exceeds its length; post-temporal spines well developed; postabdominal spines fused to form a single spine complex; lower preopercle spine directed ventrally, the upper posterio-dorsally; jaws medium; teeth small to minute; gill rakers long and numerous; in preservative abdominal region dark, trunk pigmentless

TABLE 4. COMPARISONS OF REGRESSION STATISTICS FOR THREE POPULATIONS OF *A. HEMIGYMNUS*. REGRESSION A REFERS TO PIGMENT FORM A (SEE TEXT); REGRESSION B REFERS TO PIGMENT FORM B. NS INDICATES NO SIGNIFICANT DIFFERENCE BETWEEN THE SLOPES OF THE TWO REGRESSIONS INDICATED.

Character	Regression A		Regression B		Slope-T-Test
	A	B	A	B	
Southern Ocean (Pacific)					
Body depth	−0.61	0.53 ± .041	0.45	0.48 ± .063	NS
Caudal peduncle width	0.52	0.07 ± .099	0.59	0.07 ± .016	NS
Jaw length	0.09	0.23 ± .026	0.68	0.21 ± .036	NS
Jaw width	−0.36	0.14 ± .020	0.01	0.13 ± .041	NS
	N = 41		N = 49		
Gulf of Mexico					
Body depth	−0.95	0.54 ± .086	1.62	0.45 ± .161	NS
Caudal peduncle width	0.30	0.09 ± .020	0.34	0.09 ± .037	NS
Jaw length	0.15	0.23 ± .050	−0.15	0.26 ± .108	NS
Jaw width	−0.33	0.14 ± .038	0.88	0.09 ± .053	NS
	N = 17		N = 10		
N Pacific (California)					
Body depth	0.38	0.51 ± .121	0.43	0.49 ± .176	NS
Dorsal blade	0.56	0.08 ± .031	0.72	0.07 ± .063	NS
Jaw length	0.60	0.21 ± .047	−0.58	0.24 ± .103	NS
Jaw width	0.30	0.11 ± .042	−0.36	0.14 ± .060	NS
	N = 14		N = 8		

except in definite patches along midline and above anal and subcaudal photophore groups.

Pigment forms. Two pigment forms designated form "A" and form "B" occur over much of the species range. Form A is characterized by distinct and clearly defined body pigmentation, while in form B the body pigmentation is quite diffuse. This pigment difference is not a function of size or sex, is intermediate in few individuals, and both forms do occur in the same catch. A morphometric analysis of three sympatric populations in several characters and meristics (Table 4; Figs. 33 and 34), plus measurements from one or the other pigment forms from other areas (Table 6) failed to show any significant difference between sympatric populations. In addition, there was no

TABLE 5. DIURNAL CAPTURE COMPARISONS OF THE TWO PIGMENT FORMS OF *A. HEMIGYMNUS* FROM VARIOUS AREAS FROM DEPTHS OF 0 M TO 1000 M. # = TOTAL NUMBER OF HAULS; # POS. = NUMBER OF POSITIVE HAULS; # 20+ = NUMBER OF POSITIVE HAULS CONTAINING 20 OR MORE INDIVIDUALS.

Locale	Pigment Form	Night			Day		
		#	# pos.	# 20+	#	# pos.	# 20+
NE Atlantic	A	41	9	2	47	20	14
(20–35°N, 0–30°W)	B	41	25	9	47	7	1
N Atlantic	A	129	15	6	102	43	22
(37–45°N, 30–70°W)	B	129	27	12	102	6	2
Gulf of Mexico	A	45*	3	1	35	19	6
and Caribbean	B	45*	4	0	35	0	0
Southern Ocean	A	58	12	3	25	19	3
	B	58	32	10	25	3	1

* 18 of these hauls were less than 200 m.

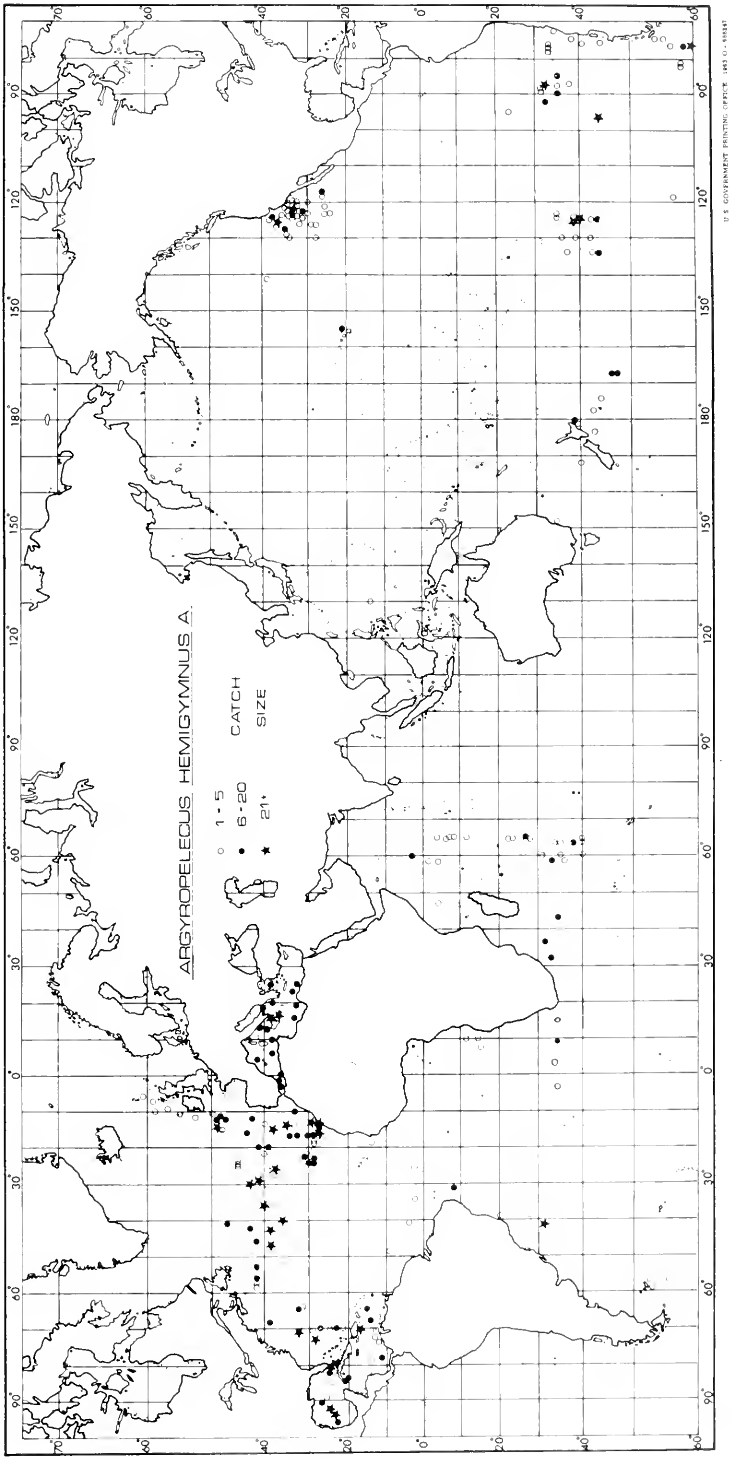


Figure 29. Horizontal distribution of *A. hemigymnus*, pigment form A. Catch size categories refer to the number of individuals taken in that haul.

consistent sorting out over the range of variability of any one form in any character. Analysis of diurnal depth distributions revealed a marked sorting out of pigment types with form A most numerous during the day while form B was predominantly caught at night (Table 5). Distributions from which Table 5 was compiled were chosen from areas where this species appears to occur throughout the horizontal sampling space. It is concluded that these two forms represent pigment states of the same species whose states can be varied individually.

Recently Badcock (1969) reported diel color variation in several mesopelagic fishes (including *A. hemigymnus*) and attributed it to a correlation with ambient light conditions. This appears to be the case in *Argyropelecus hemigymnus*. There are two anomalies, however, which raise some interesting points. First is the occurrence, occasionally in great numbers, of the day form at night and the night form during the day. Second is the relatively rare occurrence of form B in the tropics and its apparent absence from the Mediterranean (over 300 specimens examined).

Tropical submergence is present in this species (see below) and may help explain the rareness of form B in the tropics. Nevertheless, there is considerable complexity in the depth distribution of this species and if the pigment change is sensitive to small differences in ambient light, it may be used as an indication of seasonal or geographical changes in depth distribution, changes in sea water turbidity, or of other correlated information.

Distribution. Horizontal distribution (Figs. 29 and 30): Occurs in the South Atlantic around the Falkland Islands and abundantly off the southeast coast of Brazil; a scattering of catches along latitude 35°S to the Cape of Good Hope suggests a broad distribution across the South Atlantic; occurs in small catches along the southwest African coast, appears absent in the Gulf of Guinea, but occurs in the western tropical Atlantic; is taken in moderate numbers in the Caribbean and Gulf of Mexico and abundantly in the western Atlantic; is abundant across the North Atlantic and the eastern North Atlantic as far south as the Cape Verdes Islands; it represents the only species of this family in the Mediterranean, where it occurs abundantly in the western basin; scattered moderate-to-small catches are present from 5°N to 12°S latitude in the central Indian Ocean, and another population is scattered from 20°S to 40°S with several small catches reported from the southeastern and southwestern Indian Ocean; a single catch off the Philippines, another at 42°N, 169°E, and small catches from the Banda Sea and near Hawaii represent this species in the west and central Pacific; large populations occur off California and Chile; it is taken abundantly across the Southern Ocean from 35°–55°S latitude from Chile to New Zealand; taken in small numbers in the Tasman Sea and off Sidney, Australia.

Vertical distribution (Figs. 31 and 32): Occurs from 200 m to 700 m by day with the greatest concentration between 350–550 m; occurs from 100 m to 650 m by night with concentrations between 150–380 m; tropical submergence indicated in the Gulf and Caribbean by examining number of catches above 200 m (Appendix B) compared with the North Atlantic; by day it appears to concentrate at about 550 m in the Sargasso Sea (Dr. James Craddock, WHOI, personal conversation).

Geographic variation. At least seven different populations could be discerned and are identified and statistically defined for a number of characters in Tables 4 and 6 and Figures 33 and 34. Small samples from the central Pacific and Cape Verdes Islands may indicate separate populations also. Broad variations in slope between several populations were noted and these were tested for statistical significance (Table 7) indicating considerable worldwide variability and distinct population

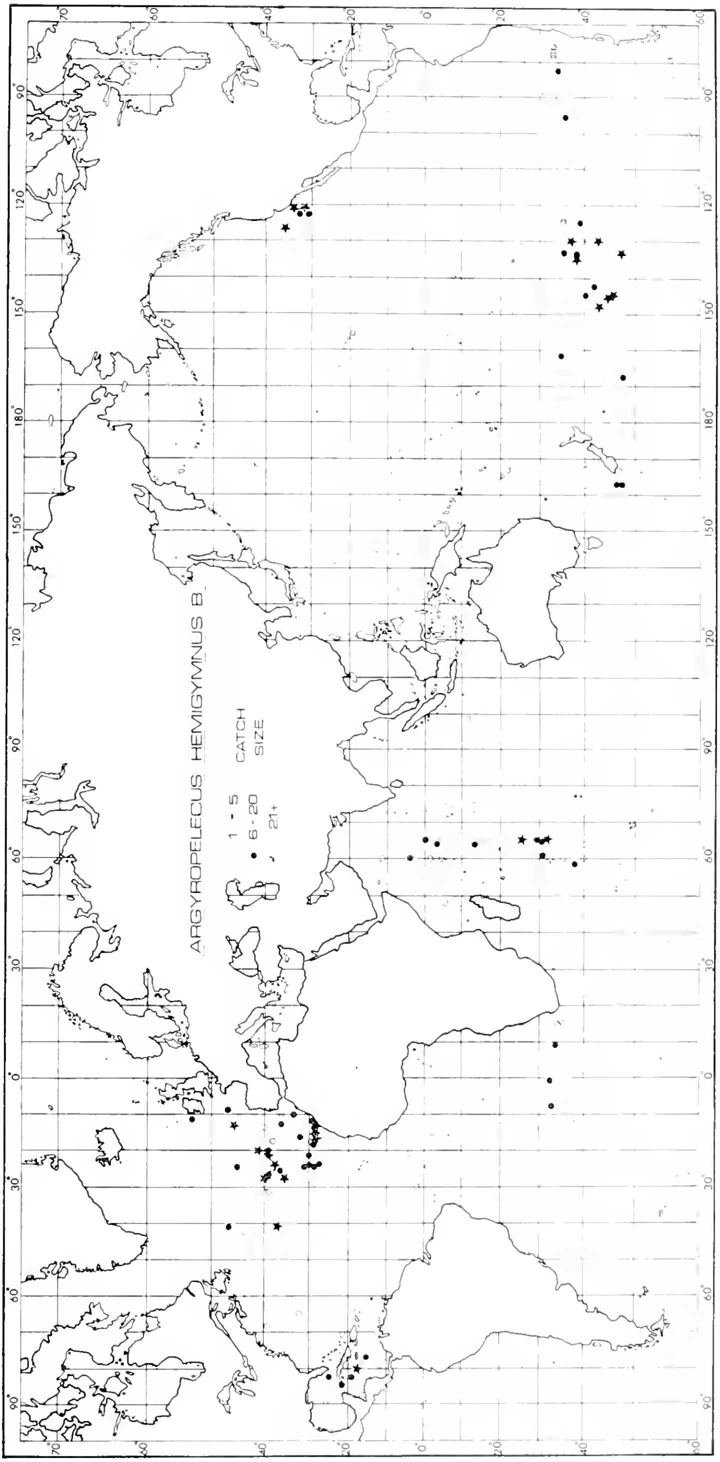


Figure 30. Horizontal distribution of *A. hemigymnus*, pigment form B.

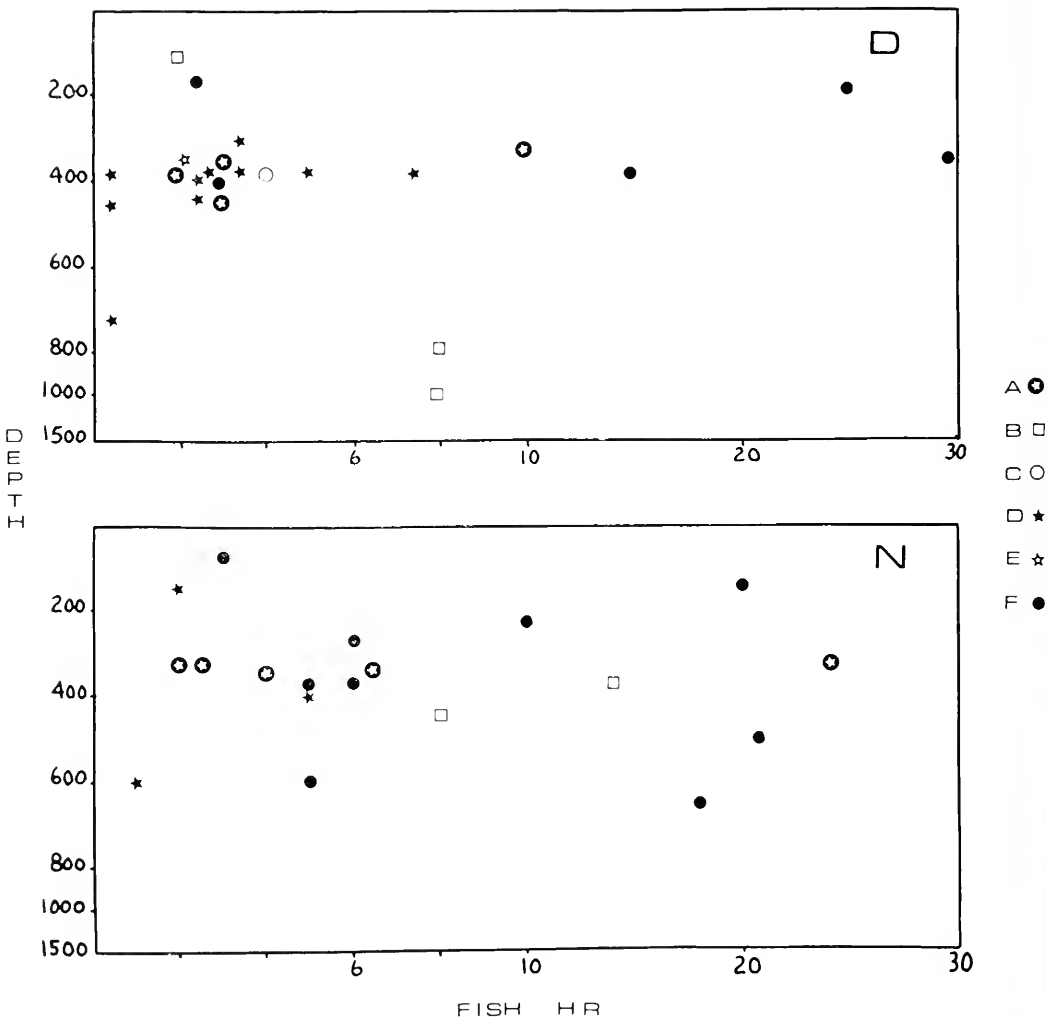


Figure 31. Diurnal vertical distribution of *A. hemigymnus*, pigment form A, determined by rate of capture with depth during the day (D) and night (N). A = Pacific (California); B = Southern Ocean; C = SW Atlantic; D = Gulf of Mexico and Caribbean; E = N Atlantic; F = NE Atlantic.

characteristics; dorsal blade height and gill raker number differences (Figs. 33 and 34) further emphasized the distinctness of populations in this species.

Argyropelecus aculeatus Valenciennes Figure 35

Argyropelecus aculeatus Valenciennes, *in* Cuvier and Valenciennes, 1849: 406 (holotype MNHNP 1817; Azores; not seen); Günther, 1864: 384; Sauvage, 1891: 483; Collett, 1903: 108; Brauer, 1906: 110; Regan, 1908: 218; Jespersen, 1915: 11; Norman, 1930: 301; Borodin, 1931: 68; Jespersen, 1934: 15; Beebe, 1937: 201; Bertin, 1940: 314 (holotype); Maul, 1949a: 17; Misra, 1952: 367; Bigelow and Schroeder, 1953: 149; Koefoed, 1961: 7; Schultz, 1961: 607; 1964: 241; Backus et al., 1965: 139; Kamohara and Yamakawa, 1965: 22; Bright and Paquegnat, 1969: 29.

Argyropelecus olfersi: Goode and Bean, 1896: 127; Jordan and Evermann, 1896: 604 (?); Rivero, 1934: 31; 1936: 56; Cervigón, 1964: 1.

Argyropelecus (Sternoptychides) amabilis Ogilby

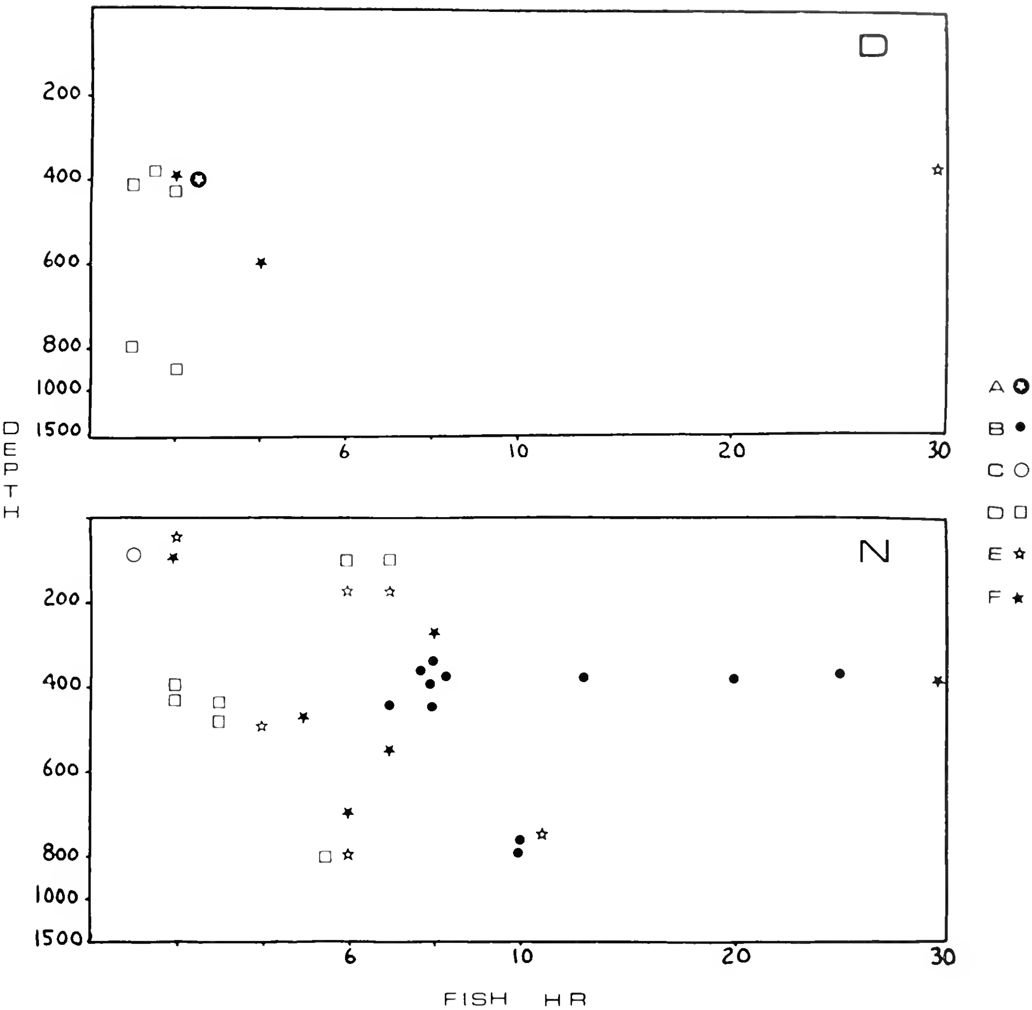


Figure 32. Diurnal vertical distribution of *A. hemigymnus*, pigment form B (see Fig. 31).

1888: 313; Goode and Bean, 1896: 127; McCulloch, 1923: 118; Whitley, 1940: 404; Koefoed, 1961: 7; Schultz, 1961: 607, 1964: 241.
Argyropelecus caninus Garman, 1899: 235.
Argyropelecus acanthurus (not Cocco) Fowler, 1936: 246; Maul, 1949b: 13; Dollfus, 1955: 24.
Argyropelecus micracanthus Parr, 1937: 49.
Argyropelecus antrorsospinus Schultz, 1937: 5.

Species distinction. See *A. olfersi* (p. 52).

Description. D. 9; A. 12; P. 10–11; total gill rakers 15–17; vertebrae 34–36.

Large species often exceeding 70 mm SL; body very deep, depth at end of dorsal less than 1.4 into SL; dorsal spine quite high, its height about equal to its length; post-temporal spines present; dorsal surface of post-temporal with distinct serrations; postabdominal spines well developed, the posterior much larger than anterior; ventral keel extends well below body margin near postabdominal spines; preopercle spines short, both pointing ventrally; jaws large, teeth long, recurved, with two enlarged canines in lower jaw; spines present below and in front of subcaudal photophores; gill rakers medium to

Table 6. Regression statistics for various populations of *A. hemigymnus*.

Character	Regression A	Regression B
NE Atlantic (36°–39°N, 27°W)		
Pigment Form B		
Body depth	1.44	0.45 ± .069
Caudal peduncle width	0.97	0.06 ± .016
Jaw length	1.69	0.17 ± .036
Jaw width	0.39	0.11 ± .035
		N = 35
NW Atlantic (36°N, 55–60°W)		
Pigment Form A		
Body depth	−0.33	0.51 ± .081
Caudal peduncle width	0.55	0.08 ± .019
Jaw length	−0.04	0.24 ± .052
Jaw width	0.43	0.12 ± .034
		N = 24
Indian Ocean (5°–35°S, 55°–65°E)		
Pigment Form B		
Body depth	−0.96	0.55 ± .266
Dorsal blade	0.35	0.11 ± .129
Jaw length	0.99	0.21 ± .158
Jaw width	0.83	0.09 ± .123
		N = 7
Mediterranean		
Pigment Form A		
Body depth	1.44	0.45 ± .104
Dorsal blade	−0.24	0.09 ± .030
Jaw length	1.16	0.20 ± .056
Jaw width	−1.38	0.19 ± .045
		N = 15

short, with dentate inner surfaces; pigment diffuse on trunk, no marked pigment on midline, pigment concentration above subcaudals present, pigmentless bar anterior to caudal peduncle in young.

Distribution. Horizontal distribution (Fig. 36): Taken abundantly in the Caribbean and Gulf of Mexico; in the western North Atlantic to about 40°N and 35°W; occurs in the northeastern Atlantic south

Table 7. Slope comparisons of regressions of several characters between various populations of *A. hemigymnus*. A = Pigment form A; B = pigment form B.

Character	Population 1	Population 2	T	P
Jaw length	Gulf of Mexico B	NE Atlantic B	2.073	.05
	Gulf of Mexico A	NE Atlantic B	2.222	.035
	NW Atlantic A	NE Atlantic B	2.211	.034
	Southern Ocean A	NE Atlantic B	2.851	.005
Jaw width	Gulf of Mexico B	Southern Ocean A	2.109	.04
Caudal peduncle depth	Gulf of Mexico A	NE Atlantic B	2.659	.01
	Gulf of Mexico A	Southern Ocean A	2.098	.05
Jaw width	Mediterranean A	California A	2.548	.021

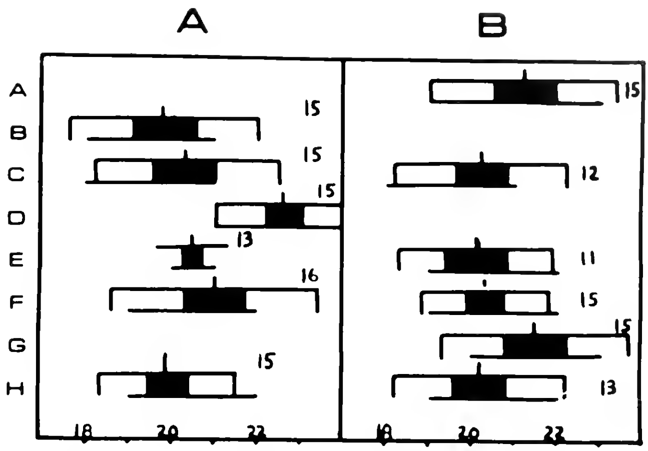


Figure 33. Geographic variation in gill raker number in *A. hemigymnus*, pigment forms A and B. A = NE Atlantic; B = NW Atlantic; C = Gulf of Mexico; D = Mediterranean; E = Indian Ocean; F = Southern Ocean (Pacific); G = N Pacific; H = Pacific (California). Numbers refer to sample size.

of about 35°N along the North African coast and associated islands; essentially absent from the tropical Atlantic; small to moderate catches in the southwestern Atlantic represent this species; taken in the central Indian Ocean from about 10°S to 40°S and reported abundant off the eastern South African coast; a few records scattered along the western Pacific from north of New Guinea to Japan represent it in the western Pacific; a number of moderate catches indicate its presence in the north central Pacific; these are matched by similar catches off Chile and one large haul off Sidney, Australia.

Vertical distribution (Fig. 37): Occurs between 200 m and 550 m by day with the greatest concentrations from 350–450 m; marked diurnal movement with major concentrations from 80–200 m at night; Sargasso Sea captures indicate concentrations at about 520 m by day (Dr. James Craddock, WHOI, personal conversation).

Geographic variation. Because of large samples available this species was used for a detailed population study in the Atlantic. It allowed checks to be made of within-population variation both from different years and as subsamples of the same catch; furthermore, an examination of samples in the northwest Atlantic provided an opportunity to look at variations over at least 15° of longitude in the same biogeographic region. Table 8 records these results. In the northwest Atlantic, results indicate that population parameters remain constant in

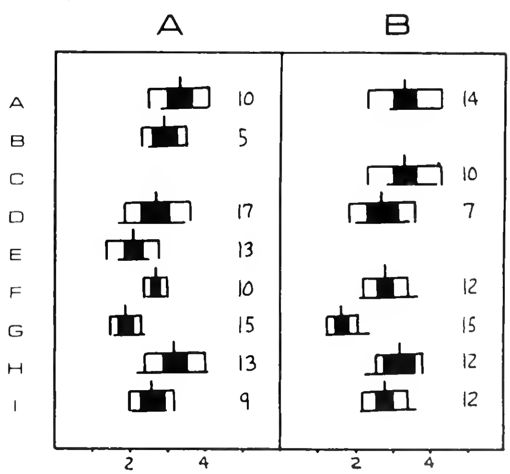


Figure 34. Geographic variation in dorsal blade height in *A. hemigymnus*, pigment forms A and B, for standard lengths 23–28 mm. A = NW Atlantic; B = Cape Verdes Islands; C = NE Atlantic; D = Gulf of Mexico; E = Mediterranean; F = Pacific (California); G = Southern Ocean; H = Indian Ocean; I = Caribbean and Tropical Atlantic. Numbers refer to sample size.

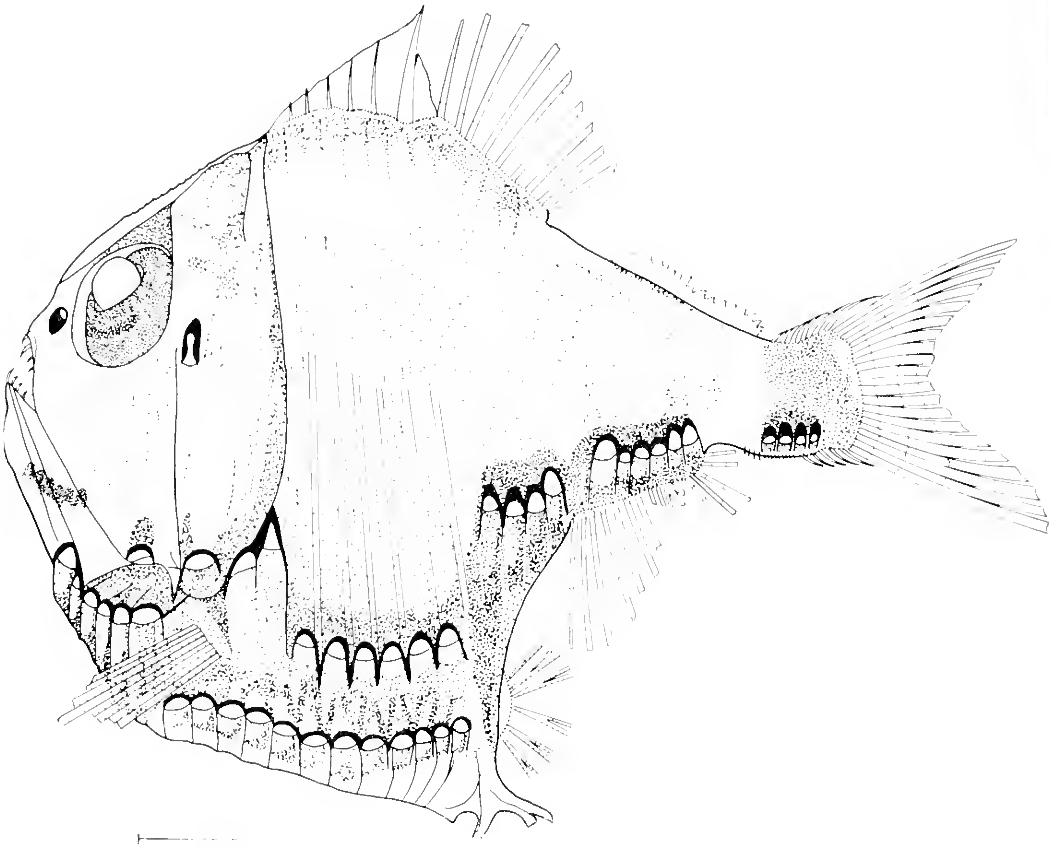


Figure 35. *Argyropelecus aculeatus;* R/V CHAIN, Cruise 60; Station 1266; SL 46 mm.

the same locality from year to year. In addition, populations in this area taken at the same latitude but separated by 15° of longitude show no indication of changes in values of parameters measured—in fact they appear to remain remarkably constant. Once again division of a large haul from the Caribbean into two subsamples gave little variability with adequate sample sizes. In a given area, populations seem to remain distinctive both from year to year and over a broad range in the same biogeographical region. There appears to be a clinal variation between populations in the Atlantic, going from the Caribbean, to the Gulf of Mexico, to the northwest Atlantic. Gill raker number and body depth (Figs. 38 and 39) show a clinal variability and possibly jaw length (Table 8) as well. Six separate populations are identified and statistically defined in Table 8 and Figures 38 and 39. The South Pacific (Chile) population is quite distinct from the others. Differences in slope between the Caribbean and northeast Atlantic populations were significant in several characters (Table 9).

Argyropelecus olfersi (Cuvier)
Figure 40

Sternoptyx olfersi Cuvier, 1829: 316 (holotype MNHNP 1889; Cape of Good Hope; not seen).

Argyropelecus olfersi, Cuvier and Valenciennes, 1849: 408; Collett, 1903: 108; Brauer, 1906: 69; Regan, 1908: 218; Zugmayer, 1911: 52;

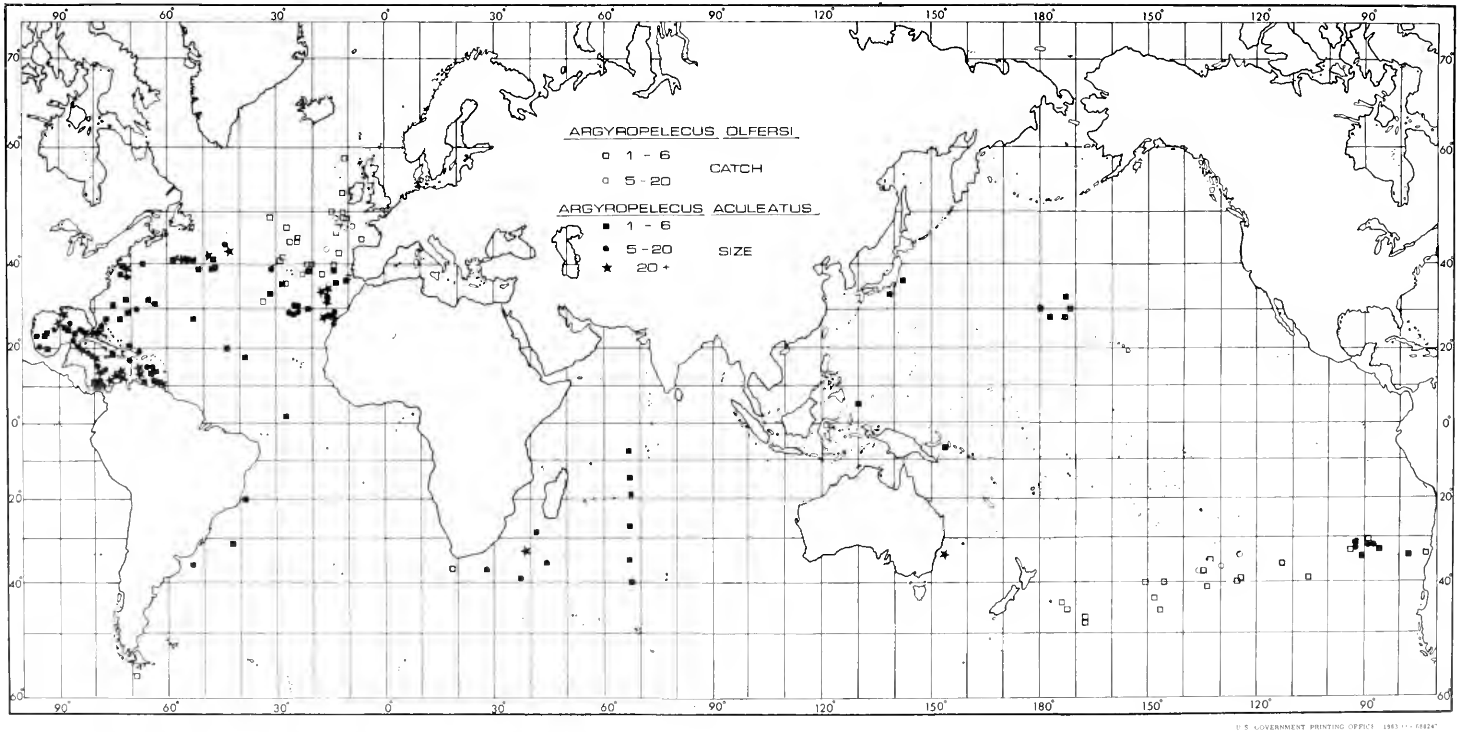


Figure 36. Horizontal distribution of *A. aculeatus* and *A. olfersi*. Catch size categories refer to the number of individuals taken in that haul.

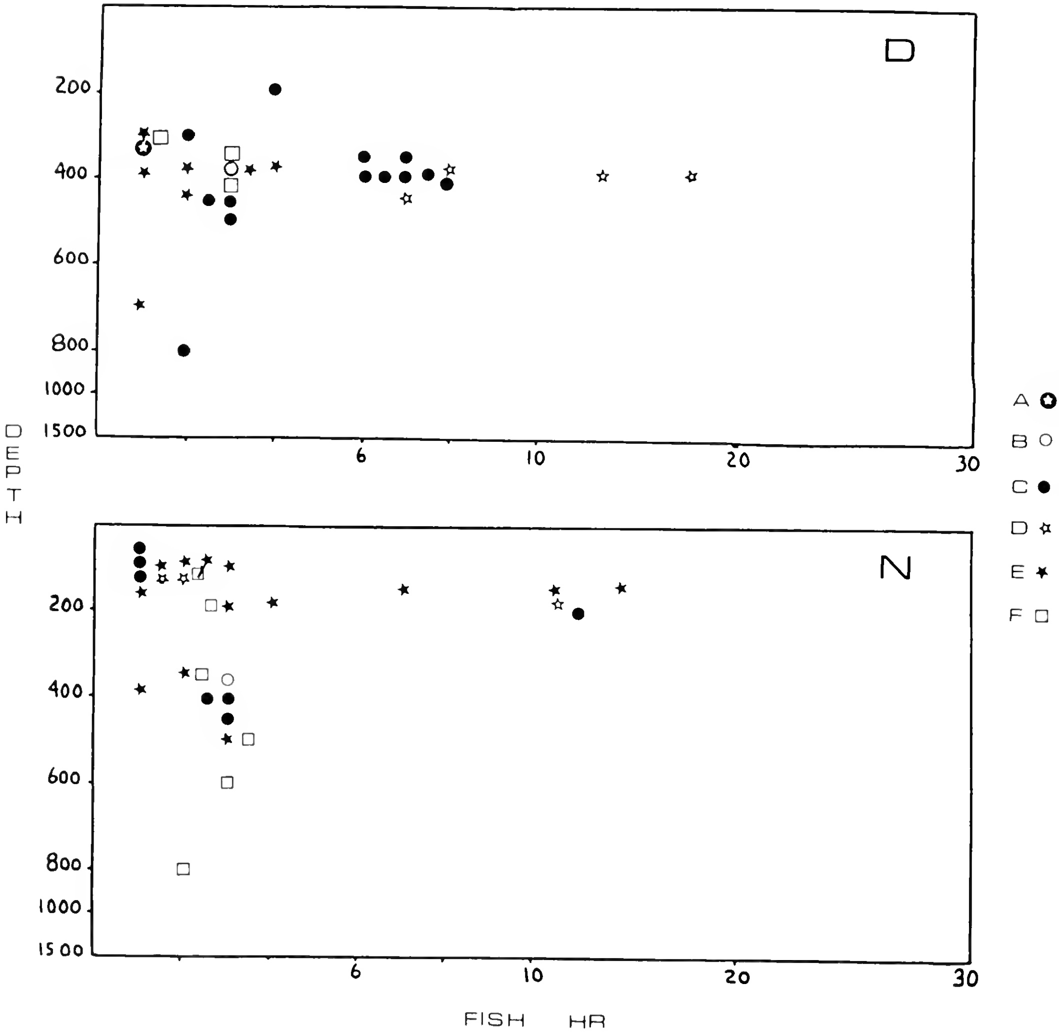


Figure 37. Diurnal vertical distribution of *A. aculeatus* determined by rate of capture with depth during day (D) and night (N). A = Pacific (Chile); B = N Central Pacific; C = Caribbean and Tropical Atlantic; D = NW Atlantic; E = Gulf of Mexico; F = NE Atlantic.

Holt and Byrne, 1913: 120; Jespersen, 1915: 23; 1934: 15; Roule and Angel, 1933: 46; Buen, 1935: 52; Parr, 1937: 49 (spines); Bertin, 1940: 314 (holotype); Nybelin, 1948: 23; Bertelsen and Grontved, 1949: 163 (light organs); Maul, 1949b: 13; Dollfus, 1955: 1; Holgersen, 1958: 120 (population density); Koefoed, 1961: 10; Schultz, 1961: 610; 1964: 241; Wheeler, 1969: 136.

Species distinction. Differs from *A. aculeatus* by absence of subcaudal spines, less deep body (see regressions, body depth, Tables 8 and 10), lower dorsal spine, higher vertebral count and post-abdominal spine characteristics; differs from *A. lychnus* by presence of enlarged canines, lighter pigment, no subcaudal spines, preopercle and post-temporal spine characteristics and first anal photophore; differs from *A. sladeni* by presence of enlarged canines; no definite pigmented

TABLE 8. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. ACULEATUS*.

Character	Regression A	Regression B
SE Pacific (Chile)		
Body depth	–1.64	0.77 ± .274
Jaw length	1.27	0.22 ± .087
		N = 8
Gulf of Mexico (24°N, 83°W)		
Body depth	0.49	0.67 ± .084
Caudal peduncle depth	0.12	0.12 ± .015
Jaw length	0.70	0.23 ± .032
		N = 23
Caribbean (13°N, 71°W) (Sample 1)		
Body depth	2.32	0.64 ± .064
Caudal peduncle depth	0.20	0.12 ± .013
Jaw length	0.70	0.24 ± .025
		N = 23
Caribbean (13°N, 71°W) (Sample 2)		
Body depth	2.85	0.63 ± .080
Caudal peduncle depth	0.39	0.11 ± .018
Jaw length	0.66	0.25 ± .034
		N = 26
NW Atlantic (42°N, 47°W) (9/64)		
Body depth	0.69	0.66 ± .087
Caudal peduncle depth	–0.06	0.12 ± .020
Jaw length	–0.05	0.26 ± .031
		N = 28
NW Atlantic (41°N, 62°W) (9/64)		
Body depth	0.60	0.67 ± .061
Caudal peduncle depth	0.23	0.12 ± .012
Jaw length	–0.17	0.26 ± .025
		N = 30
NW Atlantic (42°N, 62°W) (9/62)		
Body depth	0.25	0.67 ± .055
Caudal peduncle depth	0.57	0.11 ± .010
Jaw length	–0.47	0.27 ± .038
		N = 40
NE Atlantic (32°N, 13°W)		
Body depth	1.32	0.69 ± .123
Caudal peduncle depth	1.34	0.10 ± .019
Jaw length	–0.72	0.29 ± .042
		N = 29

TABLE 9. SLOPE COMPARISONS OF REGRESSIONS OF VARIOUS CHARACTERS BETWEEN TWO POPULATIONS OF *A. ACULEATUS*. THE CARIBBEAN POPULATION CONSISTS OF TWO SUBSAMPLES (SEE TABLE 8).

Character	Population 1	Population 2	T	P
Caudal peduncle depth	NE Atlantic	Caribbean 2	2.009	.05
Jaw length	NE Atlantic	Caribbean 1	2.266	.038
Jaw length	NE Atlantic	Caribbean 2	2.059	.048

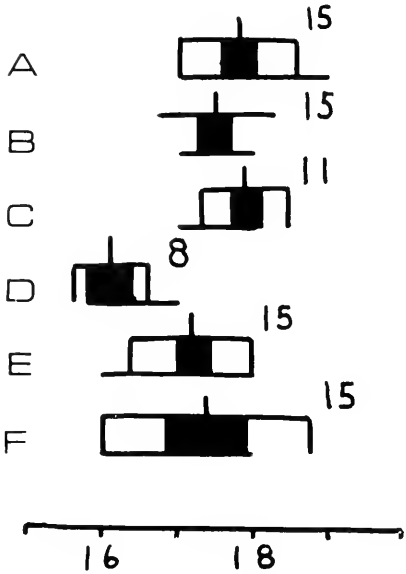


Figure 38. Geographic variation in gill raker count in *A. aculeatus*. A = NW Atlantic; B = NE Atlantic; C = N Central Pacific; D = Pacific (Chile); E = Caribbean; F = Gulf of Mexico. Numbers refer to sample size.

midline; deeper body (see regression, body depth, Table 11), spine characteristics, anal photophores, and lower gill raker count.

Description. D. 9; A. 12; P. 10–11; total gill rakers (15) 16–17; vertebrae 36–37 (38).

Large species often exceeding 70 mm SL; body deep, depth at end of dorsal usually greater than 1.5 times into SL; first preanal photophore with pointed dorsal margin; dorsal spine high, its height nearly one-half its length; post-temporal spines well developed; postabdominal spines nearly equal, anteriormost spine curves smoothly forward; lower preopercle spine long, curving forward, upper very short; jaws large; teeth recurved with two large canines in lower jaw and a somewhat smaller pair in the upper jaw; pigment diffuse over whole of trunk; no marked midline pigment spots; less marked concentration of pigment in caudal peduncle; dark pigment present on outermost caudal rays (this often lost in handling).

TABLE 10. REGRESSION STATISTICS FOR TWO POPULATIONS OF *A. OLFERSI*.

Character	Regression A	Regression B
NE Atlantic		
Body depth	0.51	0.64 ± .231
Jaw length	0.56	0.26 ± .099
		N = 8
Southern Ocean (Pacific)		
Body depth	1.74	0.61 ± .158
Jaw length	–0.19	0.28 ± .075
		N = 10

Distribution. Horizontal distribution (Fig. 36): Restricted to the northeast Atlantic between latitudes 35°N and 65°N and east of longitude 35°W; occurs in a broad band across the southern Pacific between 30°S and 50°S from Chile to New Zealand; reported southwest of the Cape of Good Hope suggesting a bipolar distribution in the Atlantic; not reported from the North Pacific or southern Indian Ocean.

Vertical distribution (Fig. 41): Data variable by day with relatively low concentrations from 200 m to 750 m; by night depths are concentrated between 200 m and 450 m with most records from 180 m to 300 m; no indications of marked geographic variation in depth.

Geographic variation. Analysis of small sample sizes from the two major widely separated populations indicate no statistical differences and little evidence of separation (Table 10; Fig. 42).

Argyropelecus sladeni Regan
Figure 43

Argyropelecus sladeni Regan, 1908: 218 (holotype BMNH; Central Indian Ocean; not seen); Jespersen, 1934: 15; Fowler, 1936: 1208; Parr, 1937: 49 (fig., incorrectly cites Norman, 1930 as original description); Norman, 1939: 19;

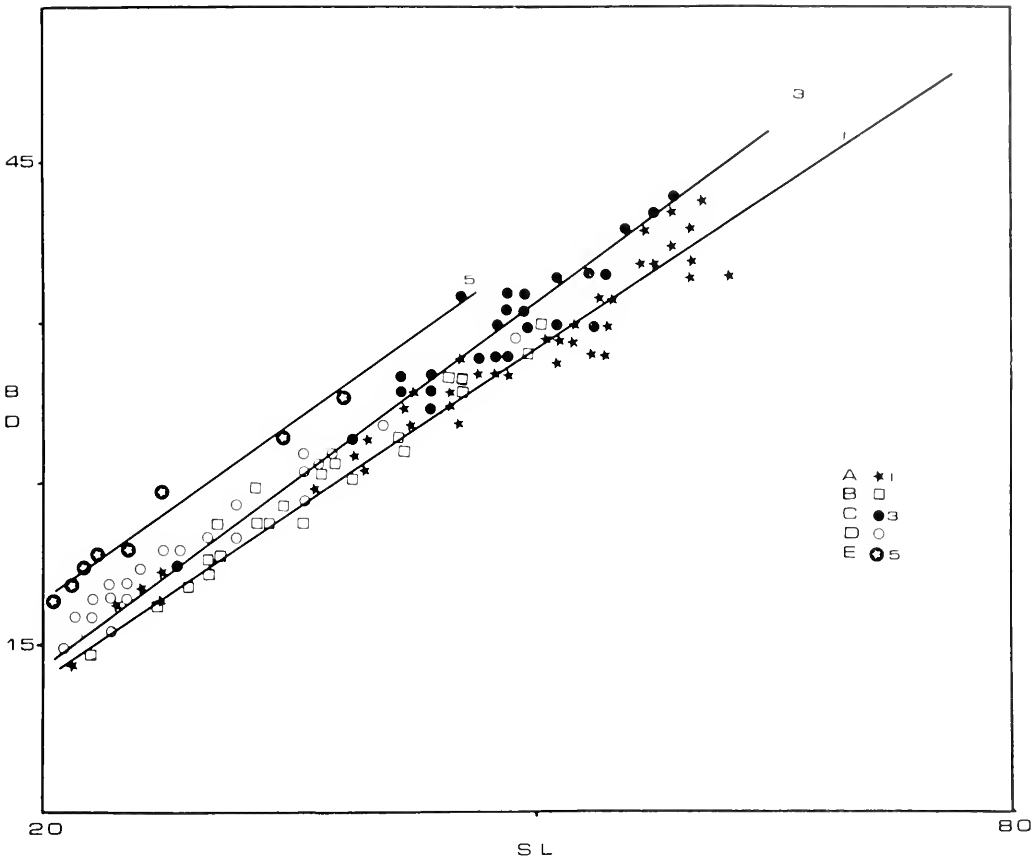


Figure 39. Geographic variation in the regression of body depth (BD) on standard length (SL) in *A. aculeatus*. A = NW Atlantic; B = Gulf of Mexico; C = NE Atlantic; D = Caribbean; E = Pacific (Chile).

Marr, 1948: 140; Misra, 1952: 367; Haig, 1955: 321; Fowler, 1956: 27; Koefoed, 1961: 1.

Argyropelecus olfersi: Barnard, 1925: 153; Smith, 1957: 37 (?); Bright and Paquegnat, 1969: 29.

Argyropelecus lychnus lychnus Schultz, 1961: 587 (in part); 1964: 241; Blache, 1964: 71; Backus et al., 1965: 139; Bright and Paquegnat, 1969: 30.

Argyropelecus lychnus sladeni Schultz, 1961: 587; 1964: 241 (incorrectly cites Norman, 1930, as original description); Kotthaus, 1967: 22 (photo., otoliths).

Argyropelecus lychnus hawaiensis Schultz, 1961: 587; 1964: 241.

Argyropelecus hawaiensis Berry and Perkins, 1965: 625; Lavenberg and Ebeling, 1967: 185.

Species distinction. See *A. olfersi* (p. 52) and *A. lychnus* (p. 63).

Description. D. 9; A. 12; P. 10–11; total gill rakers 17–21; vertebrae 35–37.

Medium size species seldom exceeding 60 mm SL; body less deep, depth at end of dorsal about two or more times into SL; dorsal blade low, height about three or more times into its length; postabdominal spines of equal size, anterior one occasionally straight, usually squared or blunted; upper preopercle spine long, directed posteriorly and usually dorsally, lower directed ventrally and often slightly posteriorly; jaws medium; teeth small, recurved, no large canines present; gill rakers medium to long, slightly dentate; first preanal photophore raised well above second

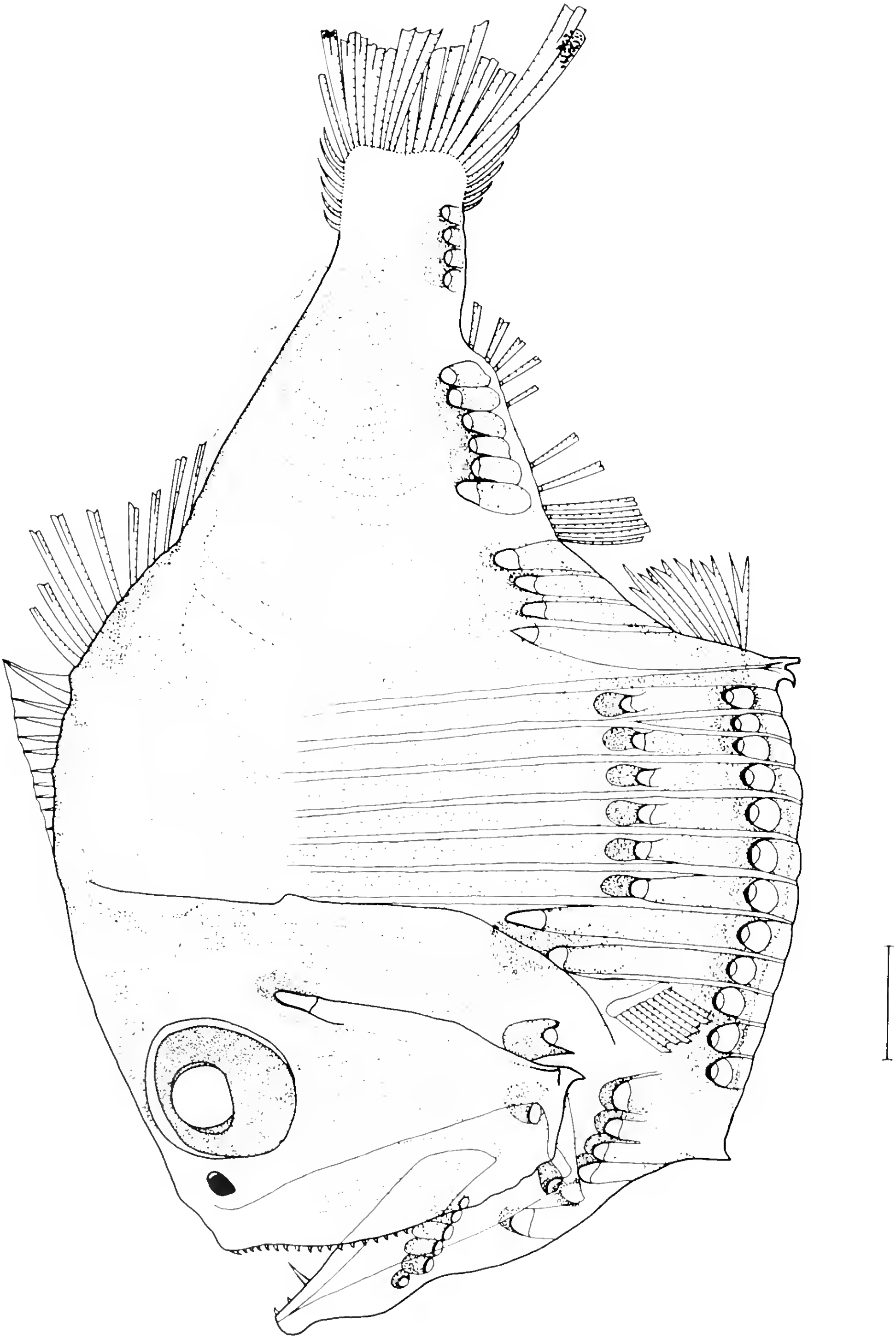


Figure 40. *Argyropelecus olfersi;* R/V ATLANTIS II, Cruise 13; Station 1039; SL 50 mm.

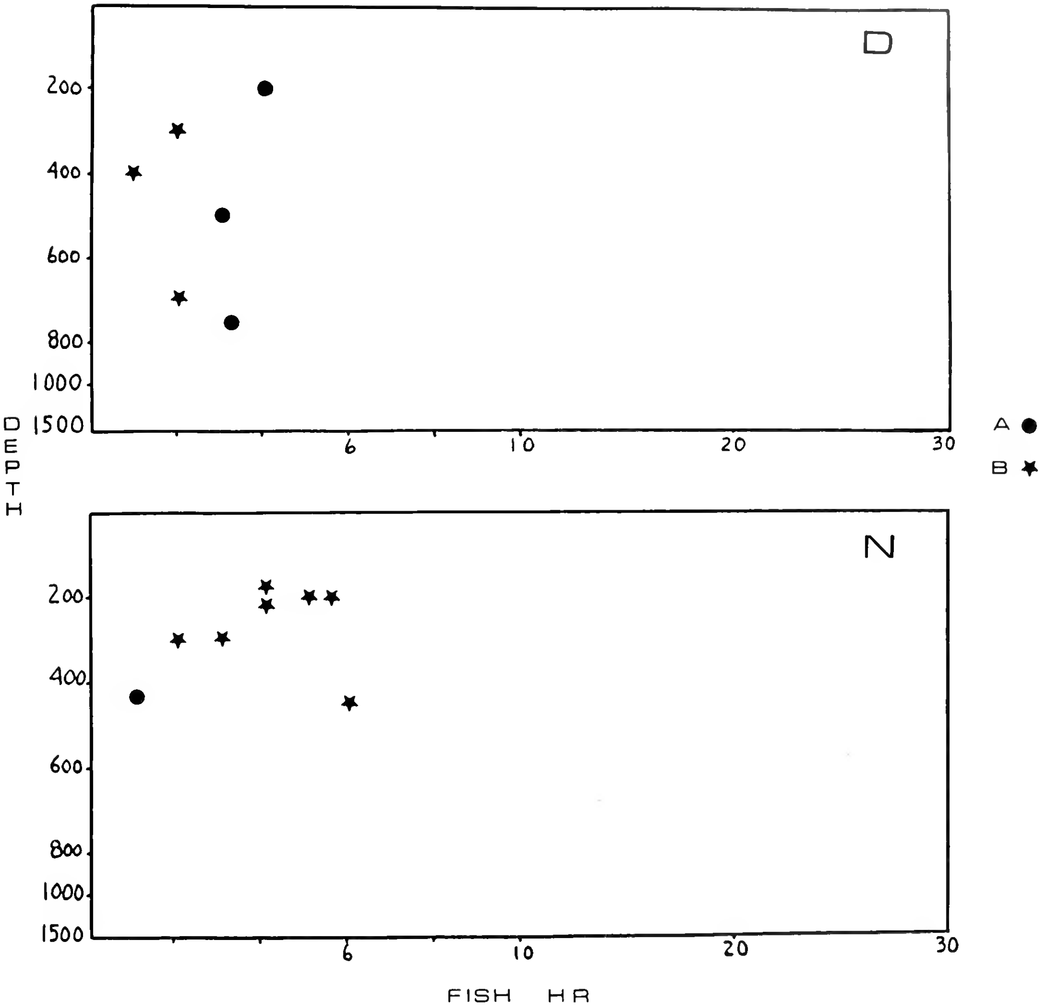


Figure 41. Diurnal vertical distribution of *A. olfersi* determined by rate of capture with depth. A = Southern Ocean (Pacific); B = NE Atlantic.

which is even with or above third; anal pterygiophore gap with three haemal spines lacking pterygiophores; in preservative pigment often quite dark; large distinct pigment spots present along midline, especially evident in smaller specimens; there may be a diurnal pigment difference similar to *A. hemigymnus* in this species.

Distribution. Horizontal distribution (Fig. 44): In the Atlantic this species is found in abundance along the African coast from about 15°S northward into the Gulf of Guinea; it occurs in moderate numbers across the equatorial Atlantic in a belt from 5°S to 15°N latitude; it is abundant in the Caribbean in the vicinity of the Venezuelan coast, absent from the northern Caribbean, appearing again in numbers in the western and northern Gulf of Mexico and the straits of Florida; a few small catches have been taken in the North Atlantic and along the Brazilian coast. In

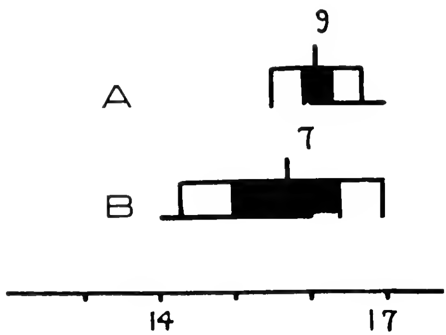


Figure 42. Geographic variation in gill raker count in *A. olfersi*. A = NE Atlantic; B = Southern Ocean. Numbers refer to sample size.

the Pacific a somewhat biantitropical distribution is indicated, with large populations represented in the North Pacific to about 175°W longitude, and off the California coast; another large population occurs off the coast of Chile; the species occurs north of New Zealand and south of Hawaii. *A. sladeni* is abundant in the northern Indian Ocean to about 15°N and along the African coast to about 10°S; while not reported from the Bay of Bengal, it is represented by several small catches south of Java.

Vertical distribution (Fig. 45): Concentrated between 350 m and 600 m by day, with the major concentrations between 350 m and 450 m; by night concentrated between 100 m and 375 m, with the major concentrations between 100 m and 300 m; no marked indication of geographic variation with depth.

Geographic variation. This species, like *A. gigas*, has low variability in those body

TABLE 11. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. SLADENI*.

Character	Regression A	Regression B
N Pacific (42°N, 165°W)		
Body depth	0.38	0.52 ± .156
Dorsal blade	2.02	0.01 ± .027
Jaw length	–0.03	0.25 ± .076
Jaw width	0.48	0.13 ± .070
		N = 10
E Pacific (California)		
Body depth	1.25	0.53 ± .074
Dorsal blade	2.62	0.00 ± .022
Jaw length	0.92	0.23 ± .027
Jaw width	0.62	0.10 ± .028
		N = 27
Indian Ocean (05°N, 65°E)		
Body depth	0.80	0.56 ± .142
Dorsal blade	1.89	0.01 ± .010
Jaw length	0.22	0.24 ± .069
Jaw width	–0.73	0.13 ± .043
		N = 11
Caribbean		
Body depth	0.87	0.52 ± .163
Dorsal blade	1.29	0.02 ± .013
Jaw length	–0.07	0.26 ± .081
Jaw width	0.75	0.12 ± .044
		N = 9
Gulf of Guinea		
Body depth	–0.91	0.57 ± .110
Dorsal blade	1.89	0.01 ± .014
Jaw length	–0.33	0.27 ± .055
Jaw width	1.14	0.11 ± .027
		N = 13
SE Pacific (Chile)		
Body depth	0.51	0.54 ± .097
Dorsal blade	2.04	0.01 ± .012
Jaw length	1.04	0.23 ± .040
Jaw width	–0.63	0.14 ± .035
		N = 16

TABLE 12. COMPARISONS BETWEEN MEAN SLOPES OF TWO CHARACTERS FOR ALL POPULATIONS OF *A. SLADENI* AND *A. LYCHNUS* FOR WHICH REGRESSION STATISTICS WERE CALCULATED. POP. # = NUMBER OF POPULATIONS; $\bar{x}$ SLOPE = UNWEIGHTED MEAN SLOPE; TOTAL # = TOTAL NUMBER OF FISH MEASURED OVER ALL POPULATIONS.

Species	Character	Pop. #	$\bar{x}$ Slope	Range	Total #
A. sladeni	body depth	6	0.54	0.52–0.57	86
A. lychnus	body depth	3	0.61	0.57–0.64	38
A. sladeni	jaw width	6	0.12	0.10–0.14	86
A. lychnus	jaw width	3	0.15	0.14–0.16	38

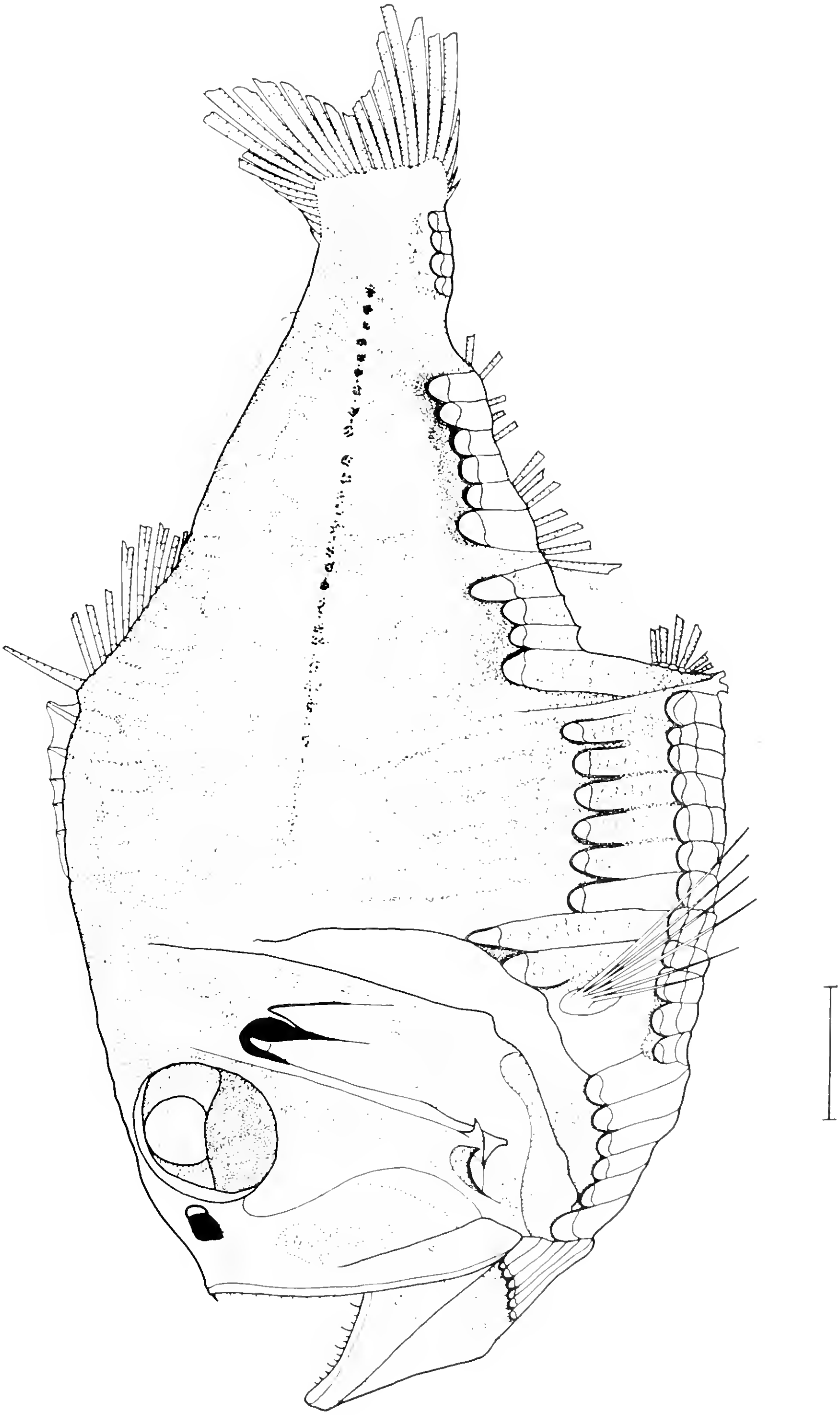


Figure 43. *Argyropelecus sladeni;* R/V CHAIN, Cruise 60; Station 1296; Sl 43 mm.

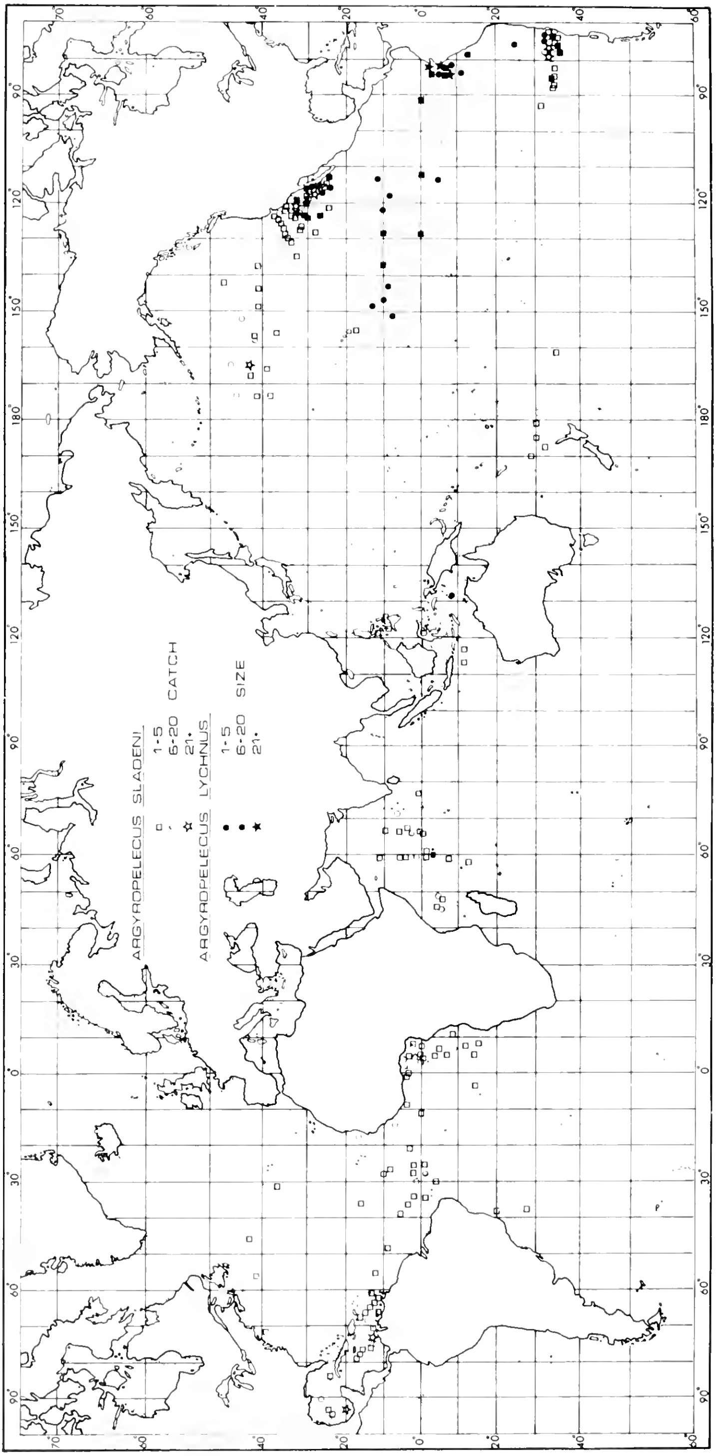


Figure 44. Horizontal distribution of *A. sladeni* and *A. lychnus*. Catch size categories refer to the number of individuals taken in that haul.

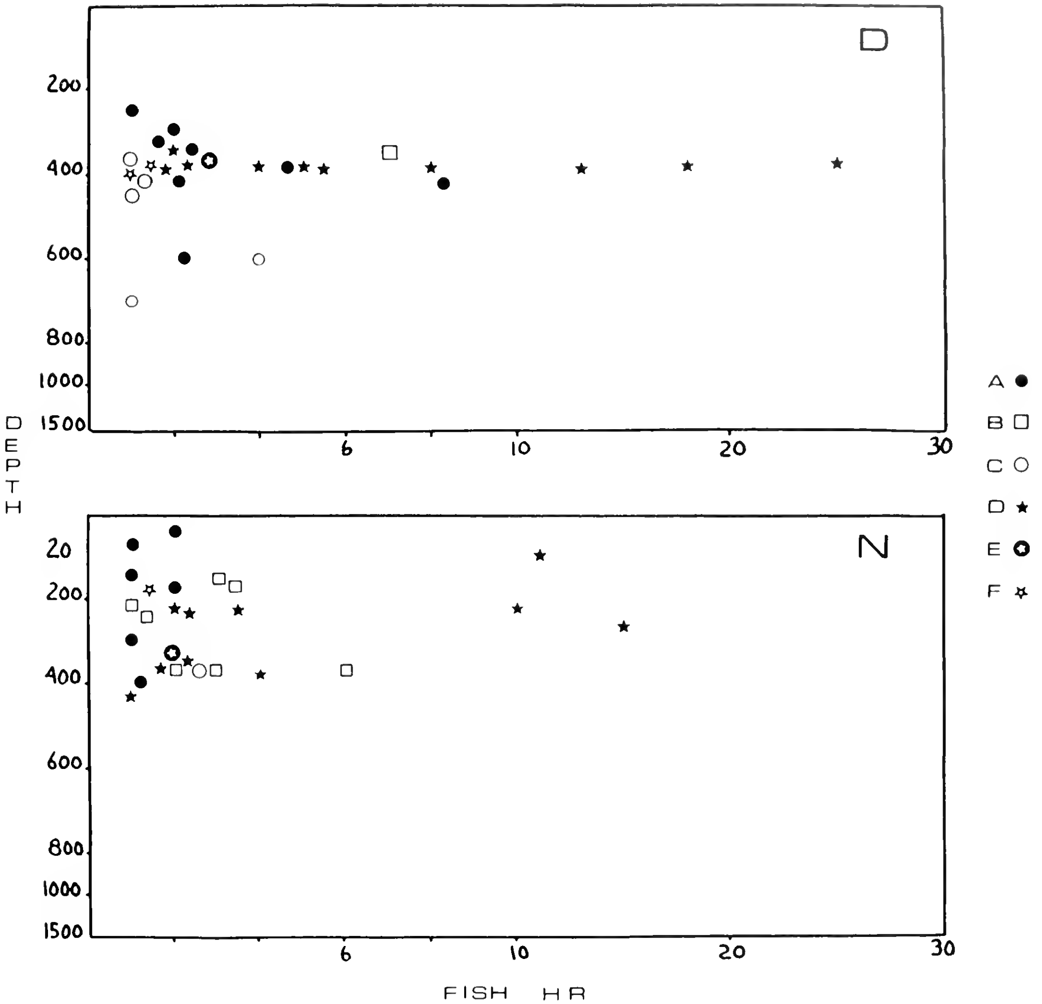


Figure 45. Diurnal vertical distribution of *A. sladeni* determined by rate of capture with depth during day (D) and night (N). A = Pacific (California); B = Pacific (Chile); C = Gulf of Guinea; D = Gulf of Mexico and Caribbean; E = N Central Pacific; F = N Atlantic.

proportions measured. Overlap is broad and sample sizes are small. Six populations were statistically defined (Table 11; Fig. 46) but only gill raker counts gave much separation. Certainly the Atlantic population is distinct from the Indian Ocean and several Pacific populations; within the latter, distinctions are not marked. The Indian Ocean, Chile, and California populations show some separation, although not statistically significant. Other characters and larger sample sizes are required to better define populations in this species.

Argyropelecus lychnus Garman
Figure 47

Argyropelecus lychnus Garman, 1899: 234 (lectotype USNM 57885, designation Schultz, 1961; tropical east Pacific, not seen; paralectotype MCZ 35193, seen); Ledenfeld, 1905: 170 (light organs); Berry and Perkins, 1965: 625; Grandperrin and Rivaton, 1966: 36; Lavenberg and Ebeling, 1967: 185.

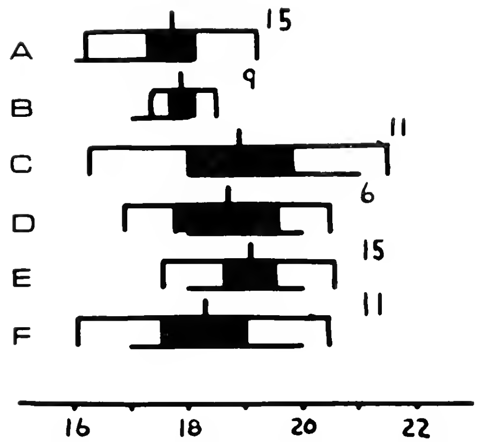


Figure 46. Geographic variation in gill raker count in *A. sladeni*. A = Gulf of Guinea; B = Caribbean; C = Indian Ocean; D = N Central Pacific; E = Pacific (Chile); F = Pacific (California). Numbers refer to sample size.

Argyropelecus olfersi: Weber and DeBeaufort, 1913: 1 (?); Clemens and Wilby, 1949: 106; Koumans, 1953: 186 (?); Morrow, 1957: 56; Koepcke, 1962: 145; Bussing, 1965: 185.
Argyropelecus lychnus lychnus Schultz, 1961: 587 (in part); 1964: 241.
Argyropelecus sp., Kotthaus, 1967: 11 (?) (photo.).

Species distinction. See *A. olfersi* (p. 52); differs from *A. sladeni* by its higher dorsal blade, preopercle spine characteristics, presence of two rather than three haemal spines in anal pterygiophore gap, lack of distinct dark pigment spots on midline, broader body, and generally lower gill raker count (Figs. 46 and 49). Tables 12 and 13 and Figure 50 illustrate the nature and degree of difference in several of the characters mentioned above.

Description. D. 9; A. 12; P. 10–11; total gill rakers 16–18; vertebrae 35–37.

Medium to large species often exceeding 60 mm SL; body deep, depth at end of dorsal greater than 1.5 into SL; dorsal blade high, height about 2.5 times into its length; postabdominal spines of about equal size, anterior one slightly smaller, not smoothly curving but blunted or squared; upper preopercle spine long, directed posteriorly and usually ventrally; lower spine usually curved slightly anteriorly or straight down; jaws large, teeth recurved especially in lower jaw, no large canines; gill rakers medium to short, dentate; first preanal photophore usually lower than third; spiny scales present in adults below subcaudal photophores; the gap made by the anal pterygiophores contains two haemal spines lacking pterygiophores; in preservative, pigment dark dorsally, diffuse on trunk with small, light pigment spots on midline.

Distribution. Horizontal distribution (Fig. 44): Absent from the Atlantic; represented possibly by a single sample from the Indian Ocean (04°S, 60°E, Kotthaus, 1967). Pri-

TABLE 13. SLOPE COMPARISONS OF THE REGRESSION OF DORSAL BLADE HEIGHT ON STANDARD LENGTH FOR VARIOUS POPULATIONS OF *A. LYCHNUS* (L) AND *A. SLADENI* (S).

Character	Population 1—L	Population 2—S	T	P
Dorsal blade	C Pacific	Chile	3.179	.005
	C Pacific	N Pacific	2.452	.025
	C Pacific	Indian	2.904	.01
	Chile	Chile	3.903	.001
	California	Chile	3.965	.001
	Chile	N Pacific	2.171	.045
	Chile	California	3.514	.001
	Chile	Indian	3.366	.005
	California	N Pacific	2.272	.035
	California	California	3.355	.005
	California	Indian	3.444	.005

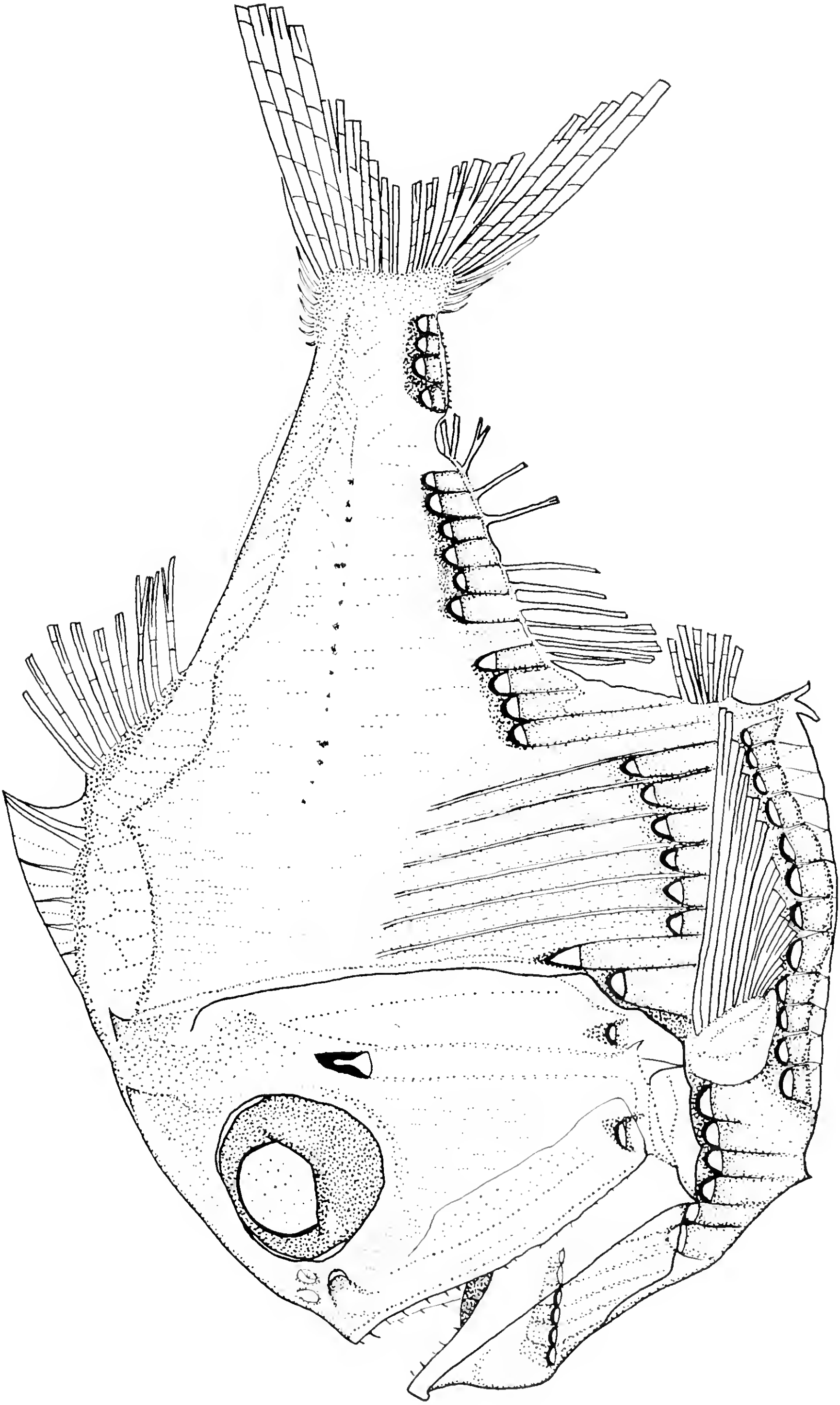


Figure 47. *Argyropelecus lychnus;* R/V HUGH M. SMITH, Cruise 31; Station 50; SL 40 mm.

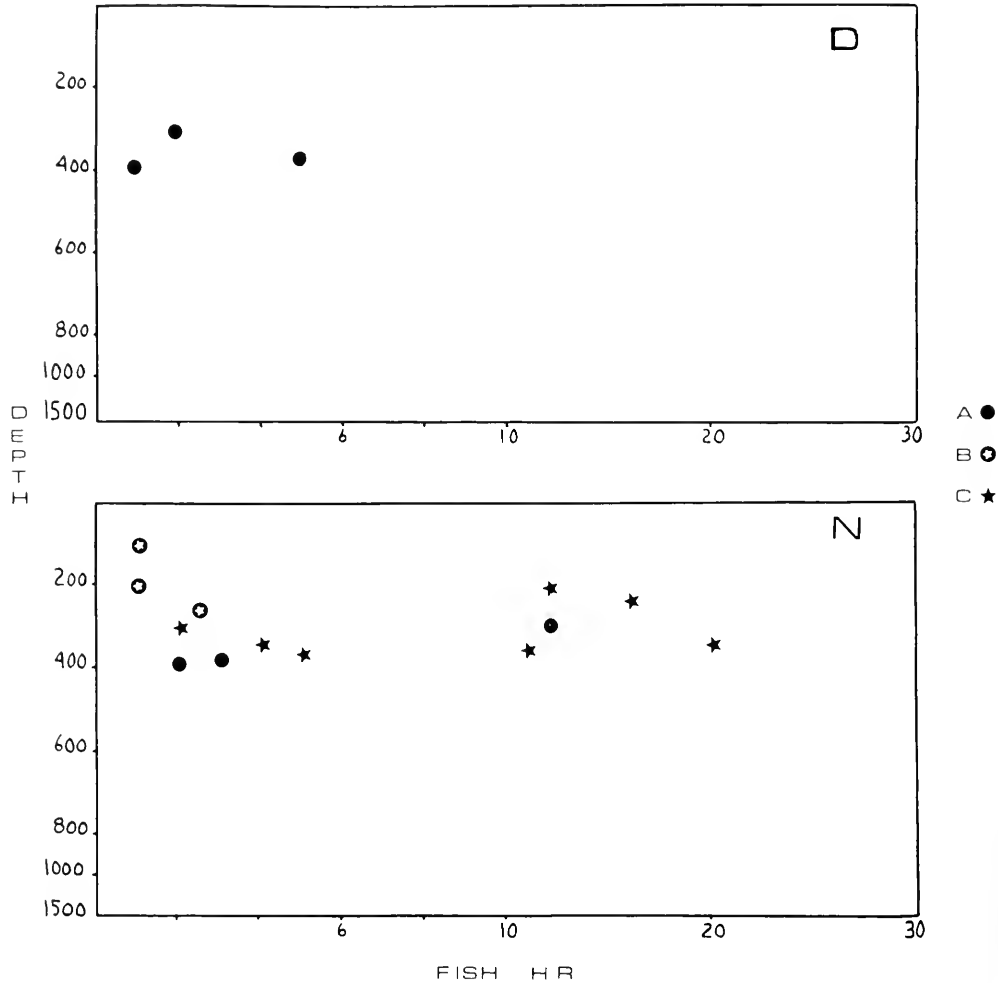


Figure 48. Diurnal vertical distribution of *A. lychnus* determined by rate of capture with depth during the day (D) and night (N). A = Pacific (California); B = Pacific (Chile); C = Tropical E Pacific.

marily restricted to the tropical Pacific; found in abundance in the eastern Pacific between 35°N and 35°S; distribution narrows across the equatorial Pacific as far as 160°W; a moderate catch from the lesser Sunda Islands indicates a possible trans-equatorial distribution in the Pacific.

Vertical distribution (Fig. 48): Concentrated between 300 m and 400 m off California by day, with the highest concentration near 400 m; by night major concentrations occur from 200 m to 350 m, with no marked indication of geographical variation in depth.

Geographic variation. Three samples from widely separated areas in the tropical east Pacific and its northern and southern boundaries gave no indication of any significant variation (Table 14; Fig. 49). Horizontal distribution data indicates an essentially continuous distribution in this area.

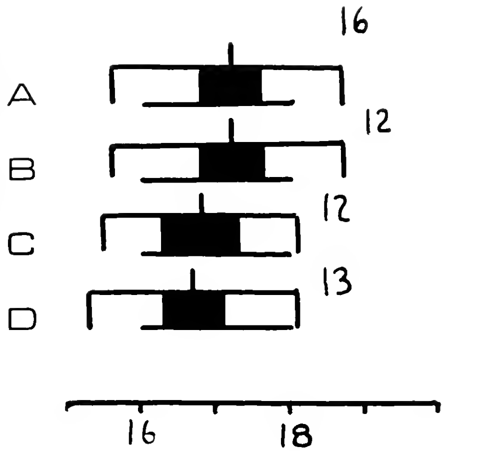


Figure 49. Geographic variation in gill raker count in *A. lychnus*. A = Central Pacific; B = Tropical E Pacific; C = Pacific (Chile); D = Pacific (California). Numbers refer to sample size.

Genus *Sternoptyx* Hermann, 1781

Sternoptyx Hermann, 1781: 8 (type species: *Sternoptyx diaphana* Hermann, 1781, by monotypy).

Diagnosis. Ten abdominal, three anal, three branchiostegal and five isthmus photophores; a single large dorsal pterygiophore spine with an anterior, serrated extension; first anal pterygiophore greatly enlarged, forms support for triangulate membrane above anal fin rays; premaxilla without anterior pedicels; anteriormost gill rakers reduced to toothed ridges; posttemporal and supracleithrum separate; hypural elements fused to form single caudal plate; haemal and neural spines greatly elongate in trunk region.

Description. Photophores: PO 1; PTO 1; PRO 1; SO 1; SP 3; PAN 3; SAN 1; AN 3; SC 4.

Spines: Preopercle with single ventrally oriented spine; retroarticular bears spine, preabdominal spine present; basipterygia fused to form a set of four postabdominal spines; base of first anal pterygiophore bears ventral spines; no well-developed post-temporal spines.

TABLE 14. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. LYCHNUS*.

Character	Regression A	Regression B
SE Pacific (Chile)		
Body depth	2.38	0.57 ± .120
Dorsal blade	1.56	0.05 ± .018
Jaw length	0.84	0.26 ± .055
Jaw width	–0.46	0.16 ± .043
		N = 12
E Pacific (California)		
Body depth	0.94	0.61 ± .107
Dorsal blade	1.53	0.04 ± .013
Jaw length	–0.15	0.29 ± .058
Jaw width	–1.02	0.16 ± .031
		N = 15
Central Pacific (10°N, 145°W)		
Body depth	1.42	0.64 ± .156
Dorsal blade	1.79	0.05 ± .023
Jaw length	0.88	0.28 ± .068
Jaw width	–0.77	0.14 ± .052
		N = 11

Eyes: Large, well developed, nontelescopic.

Gill rakers: Total seven to nine; well developed, with rough spiny margins; anteriormost rakers reduced to spiny toothlike plates extending into mouth cavity.

Jaws and dentition: Jaws vertically oriented, premaxilla small, heavily toothed; maxilla heavily toothed and major upper jaw bone in gape; lower jaw heavily toothed, teeth small, sharp, triangulate; palatine teeth present; first epibranchial extended anteriorly and ventrally forming toothed arms at dorsal, posterior end of mouth.

Meristics: Vertebrae 28–31; C. 9+10; D. 8–11; A. 14–16.

Color: Bright silvery in life, dark pigment especially evident on dorsal surface;

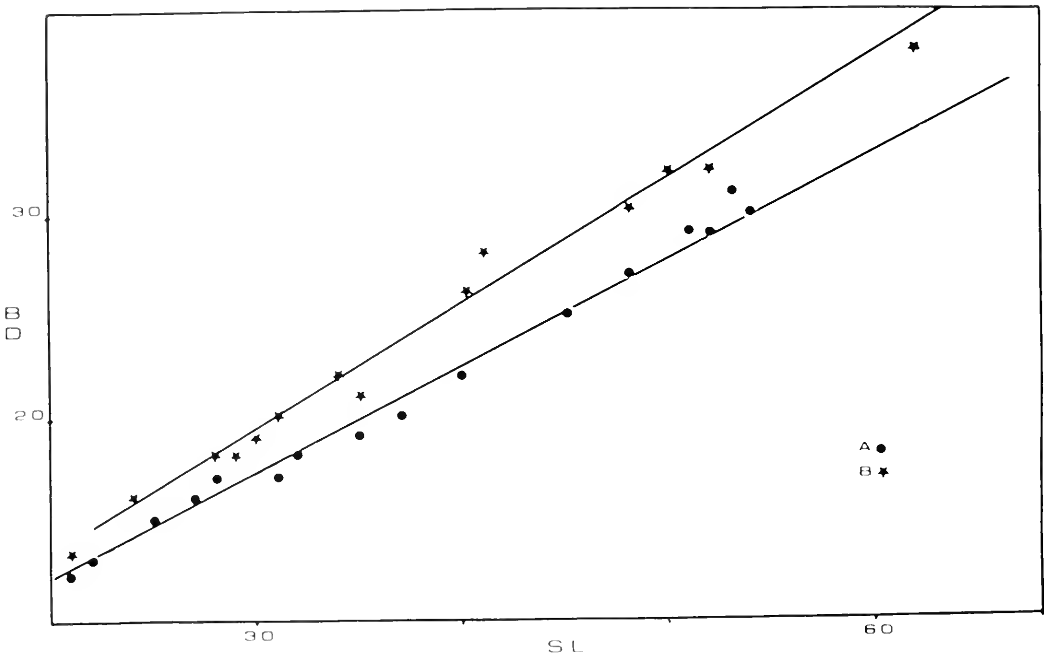


Figure 50. Regression of body depth (BD) on standard length (SL) in *A. sladeni* (A) and *A. lychnus* (B) off California.

silver quickly lost in formalin preservative; sides can be very dark, often black.

Internal anatomy: Air bladder and gas gland well developed and fills much of the body cavity (see Marshall, 1960); digestive system simple, consisting of a heavily pigmented, single sectioned stomach, capable of considerable distension, five to seven pyloric caecae of which only two to three are long and well developed, relatively small liver and short, uncoiled, thin-walled intestine. The gonads, when mature, lie against the posterior wall of the body cavity. This cavity is large, unlined with pigment, and appears capable of some expansion.

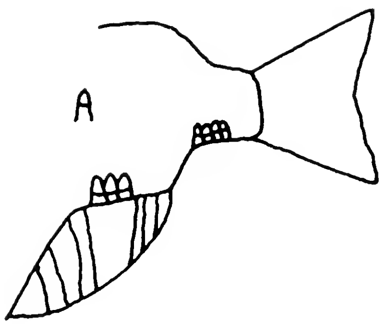
Key to the Species of *Sternoptyx*

1a. Dorsal long, its length greater than 1.3 times height of dorsal spine; trunk long and narrow, SL more than 3.0 times body depth at end of dorsal (see regression, body depth, Table 15); body very dark, pigment forms broad band at base of caudal rays .... *S. obscura* (p. 69).

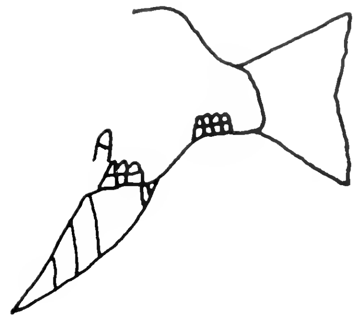
b. Dorsal short, its length less or equal to height of dorsal spine; trunk broad, SL less than 2.8 times body depth at end of dorsal (see regression, body depth, Tables 16 and 17); body pigment less uniformly dark, pigment absent or in very narrow band at base of caudal rays 2

2a. Supra-anal photophore high, its height greater than one-half the distance from ventral body margin to midline (often raised to midline); gill raker tooth plates with prominent spines; secondary anal pterygiophores long, extending posteriorly on same level as anal photophores .... *S. pseudobscura* (p. 72).

b. Supra-anal photophore low, its height less than one-half distance from ventral body margin to midline; gill raker tooth plates lacking prominent spines; secondary anal pterygiophores short; not extending posteriorly on same level as anal photophores .... *S. diaphana* (p. 75).



a.



b.

Sternoptyx obscura Garman
Figure 51

Sternoptyx obscura Garman, 1899: 63 (lectotype USNM 177888; designation Schultz, 1961; tropical east Pacific; not seen; paralectotype MCZ 28532; seen); Ledenfeld, 1905: 170 (light organs); Follett, 1952: 409.

Sternoptyx diaphana Schultz, 1961: 587 (in part); 1964: 241 (in part); Berry and Perkins, 1965: 625 (in part).

Species distinction. Differs from both *S. diaphana* and *S. pseudobscura* in its shorter dorsal spine and longer dorsal fin; longer, narrower trunk, slight extension of body

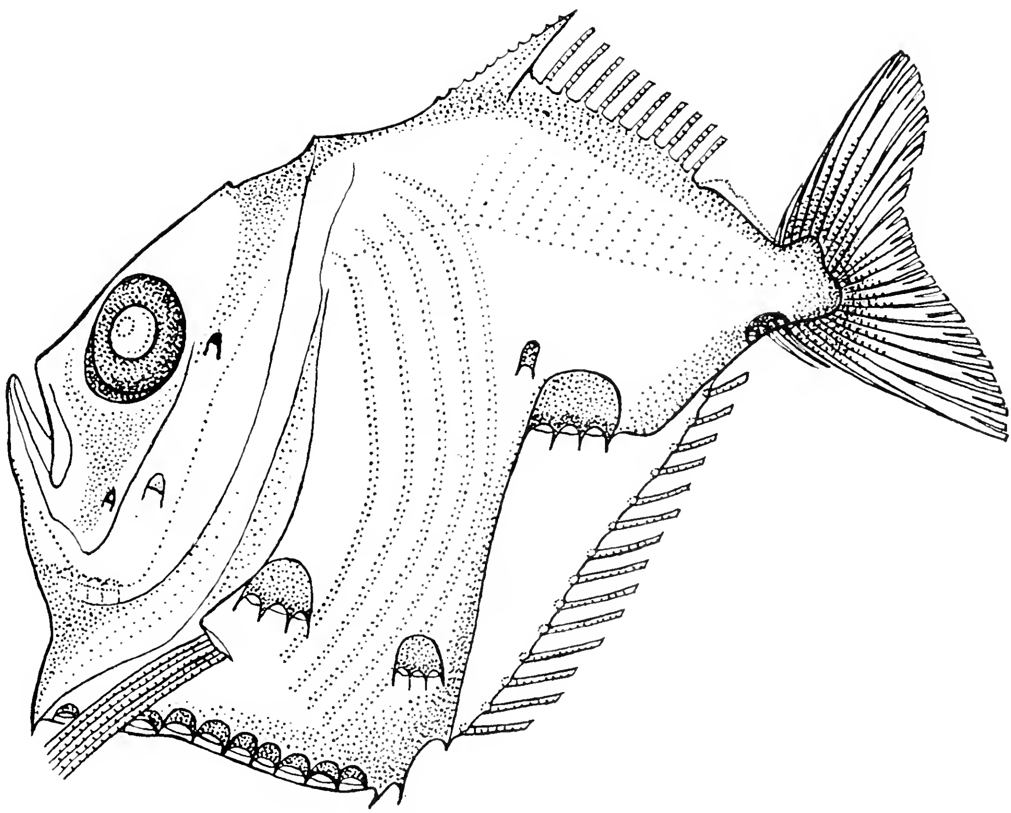


Figure 51. *Sternoptyx obscura*; R/V ANTON BRUUN, Cruise 3; Station 215; SL 30 mm.

margin in front of anal photophores, broad pigment band on base of caudal rays, and generally dark pigment; differs from *S. pseudobscura* in its lower supra-anal photophore, small teeth, low gill raker tooth plates, and smaller mouth; from *S. diaphana* in its extension of the ventral body margin at same level behind anal photophores. Tables 18 and 19, and Figures 53, 56, and 61 illustrate the degree of difference between the three species in several of the above characters. Note especially the significant differences between sympatric populations.

Description. D. 10–11; A. 14–15; P. 10–11; total gill rakers 7–9; vertebrae 29 (30).

Small species, seldom exceeds 40 mm SL; trunk long and narrow, its length usually longer than depth; dorsal fin long, its length more than 1.3 times the length of dorsal spine; abdominal length along midline from supra-anal photophore to caudal peduncle, less than or equal to body depth at end of dorsal; postabdominal and anal pterygiophore spines long; posterior anal pterygiophores extend behind and at same level with anal photophore group; supra-anal photophore raised above anals one half or less the distance to midline; body margin extends slightly in front of anal photophores before curving ventrally; jaws medium; teeth small; gill raker tooth plates consist of multiple low spiny ridges; anterior dorsal surface of tongue between branchial arches smooth; few-to-no raised nodules; in preservative, pigment very dark over whole of body; pigment extends in broad band at base of caudal fin rays.

Distribution. Horizontal distribution (Fig. 52): This species has not been recorded from the Atlantic; it is concentrated north of 10°S latitude in the Indian Ocean, although small catches occur as far as 40°S; occurs in the eastern Bay of Bengal, and abundantly south of Java; occurs off the Philippines and scattered but large catches indicate in all probability a continuous distribution across the equatorial Pacific; occurs abundantly in the tropical east Pacific from California to the Chile-Peru border.

TABLE 15. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *S. OBSCURA*.

Character	Regression A	Regression B
Indian Ocean (5°N, 60°E)		
Body depth	−0.35	0.31 ± .051
Abdominal length	−1.16	0.40 ± .074
		N = 23
Indian Ocean (3°N, 67°E)		
Body depth	0.45	0.29 ± .133
Jaw length	2.41	0.09 ± .067
		N = 10
Java (10°S, 114°E)		
Body depth	0.98	0.27 ± .071
Abdominal length	0.68	0.31 ± .090
		N = 25
Central Pacific (11°N, 163°E)		
Body length	−1.72	0.37 ± .067
Abdominal length	0.12	0.37 ± .074
Jaw length	0.85	0.14 ± .028
		N = 20
Central Pacific (7°S, 135°W)		
Body depth	−0.71	0.34 ± .104
Abdominal length	0.71	0.35 ± .141
Jaw length	0.10	0.15 ± .057
		N = 11
East Pacific (California)		
Body depth	−0.94	0.33 ± .075
Abdominal length	−1.23	0.42 ± .091
Jaw length	1.85	0.12 ± .034
		N = 15

Vertical distribution: Depth data is spotty and no depth rate plot was made, however, data (Appendix B) indicates a depth range of 650 m to at least 1000 m; tropical Pacific maximum net depth figures concur in general with this range.

Geographic variation. Analysis of catches from many widely scattered areas in the Pacific and Indian Ocean gave no indication of population variation (Table 15, Fig. 53). This, coupled with horizontal distribution data, indicates a probable single trans-Indo-Pacific population.

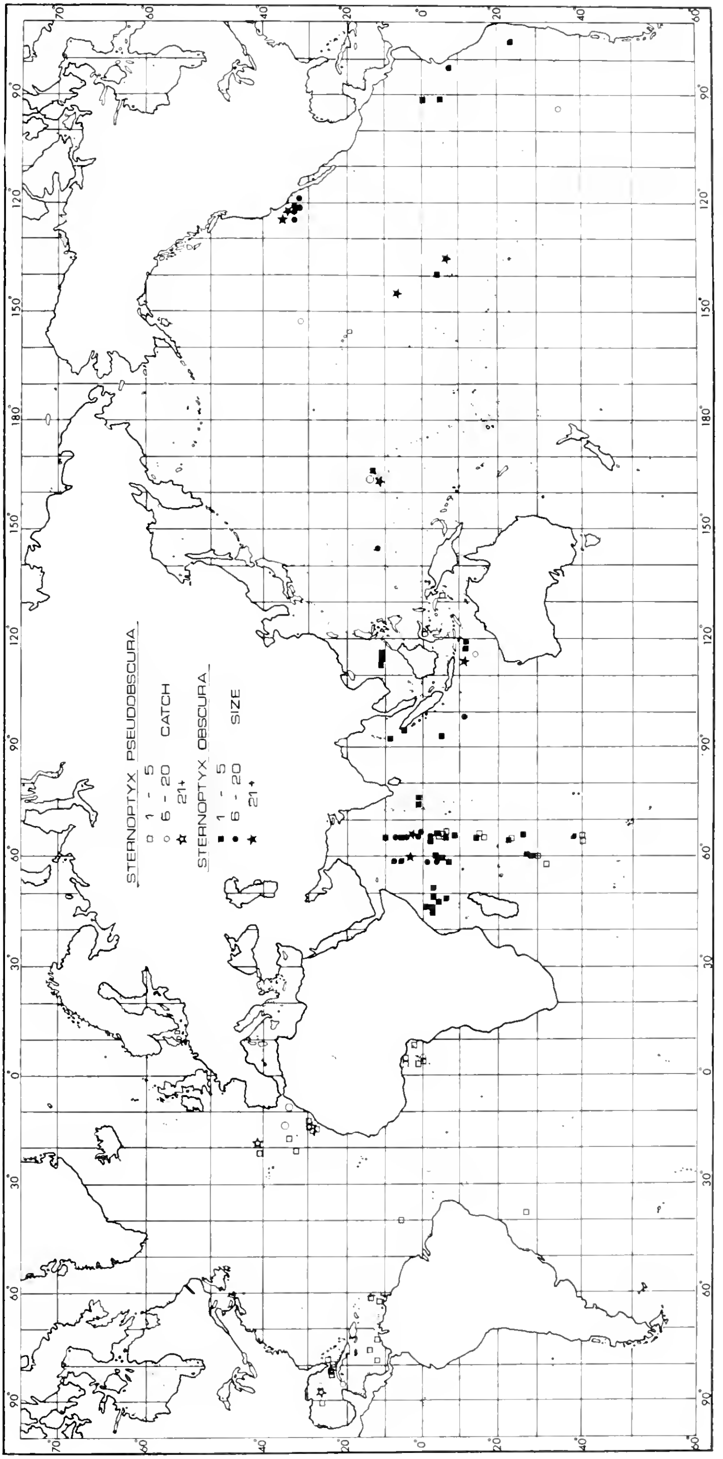


Figure 52. Horizontal distribution of S. *obscura* and S. *pseudobscura*. Catch size categories refer to the number of individuals taken in that haul.

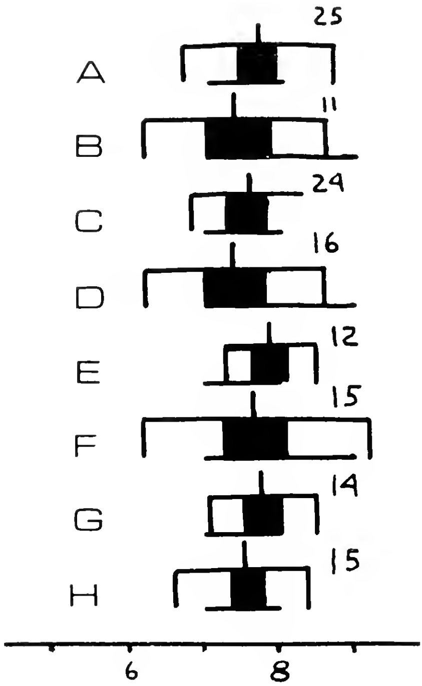


Figure 53. Geographic variation in gill raker count in S. obscura. A = E Indian Ocean; B = Central Indian Ocean; C = Tropical E Pacific; D = Banda Sea; E = Central Tropical Pacific; F = Marshall Islands; G = Pacific (California); H = Indian Ocean—S of Bali. Numbers refer to sample size.

Table 16. Regression statistics for various populations of *S. pseudobscura*.

Character	Regression A	Regression B
Gulf of Guinea		
Jaw length	1.23	0.15 ± .243
Photophore	0.43	0.19 ± .076
		N = 8
Caribbean		
Jaw length	1.70	0.15 ± .045
Photophore	2.28	0.11 ± .052
		N = 13
Florida (30°N, 76°W)		
Jaw length	1.85	0.16 ± .080
Photophore	0.58	0.15 ± .091
		N = 6
Indian Ocean (6°–35°S, 55°–65°E)		
Jaw length	2.04	0.16 ± .200
Photophore	2.21	0.17 ± .098
		N = 6
Central Pacific		
Body depth	−1.06	0.49 ± .078
Abdominal length	0.21	0.32 ± .066
Jaw length	1.63	0.15 ± .061
		N = 13

Sternoptyx pseudobscura n. sp.
Figure 54

Holotype MCZ 46400, 1° 20′S, 27° 37′W; 2/27/63; R/V CHAIN, Cruise 35; Station 977.

Sternoptyx diaphana: Brauer, 1906: 69 (in part); Maul, 1949b (in part); Blache, 1964: 71; Backus et al., 1965: 139 (in part).

Species distinction. See *S. obscura* (p. 69), differs from *S. diaphana* by its larger mouth (see jaw length, Fig. 62), longer teeth and gill raker tooth plate spines; markedly higher supra-anal photophore; extension of long anal pterygiophores behind and at same level with anal photophores. Tables 18 and 19, and Figures 56, 61, and 62 illustrate the nature and degree of difference between the two species.

Description. D. 10–11; A. 14–16; P. 10–11; total gill rakers 7–9; vertebrae 29.

Largest species in genus, often exceeds 55 mm SL; trunk broad, its depth greater than length; dorsal spine long, its length about equal to, or less than, length of dorsal fin; posterior anal pterygiophores long, extend behind and at same level as anal photophores; supra-anal photophore very high, its height more than one-half the distance from ventral body margin to midline (often raised to midline); no body margin extension in front of anal photophores; jaws large; teeth well developed and recurved; gill raker tooth plates with long spines; usually one much longer than others; anterior dorsal surface of tongue with small nodules; postabdominal and anal pterygiophore spines long; in preservative, pigment dark over most of body except lighter in trunk region; if present, pigment band very narrow at base of caudal rays.

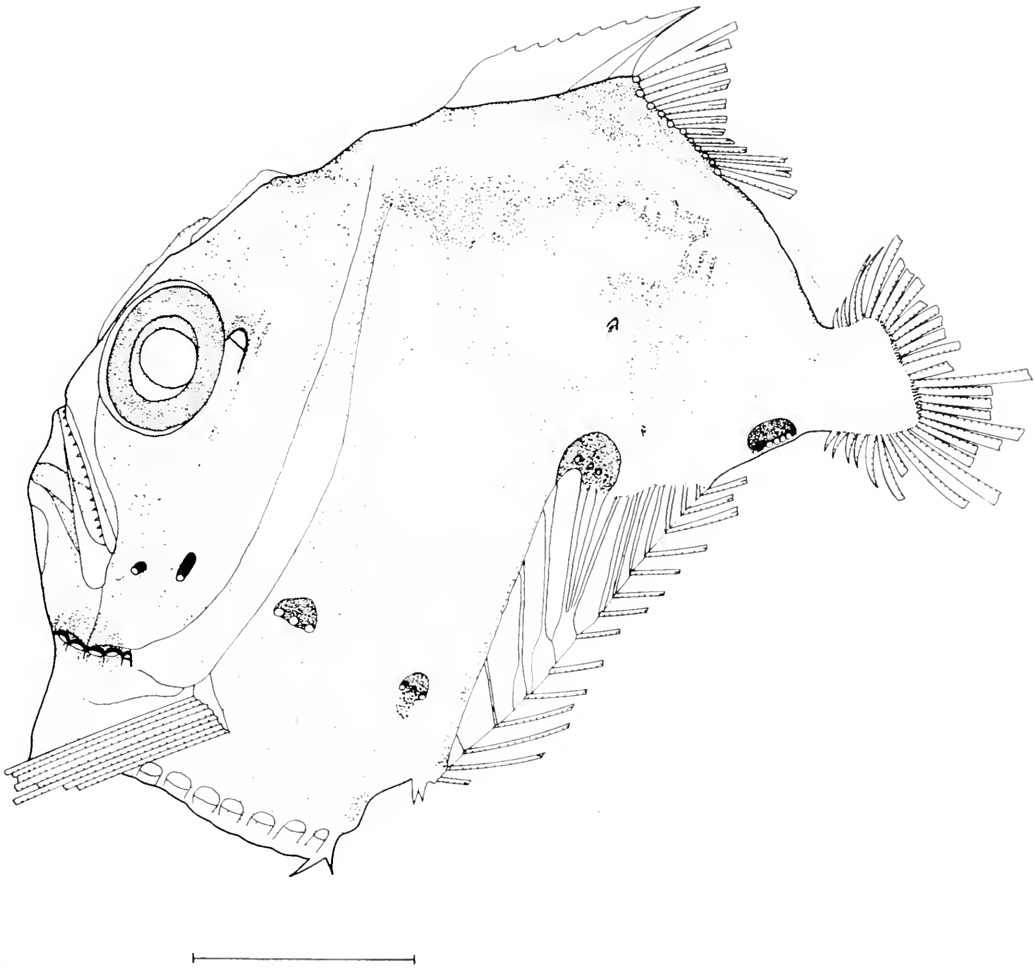


Figure 54. *Sternoptyx pseudobscura*; R/V CHAIN, Cruise 60; Station 1310; 22 mm.

Holotype: measurements (mm), SL 43.1, BD 15.0, JL 07.4, CP 04.6, Ab. length 14.0; meristics: GR 7, D 9, A 15, anal photophores 3; name derivation: *pseudobscura* refers to this species' close resemblance to *S. obscura*.

Distribution. Horizontal distribution (Fig. 52): The limited distributions seen here may be artifacts resulting from the vertical distribution of this species; widely scattered but moderate-to-high catch numbers are additional indications of sampling problems. This species occurs in the South Atlantic off Brazil, and in the Gulf of Guinea off Africa with widely scattered occurrences in the tropical Atlantic; it is abundant in the northern Gulf of Mexico and the straits of Florida; scattered catches indicate its presence in the southern Caribbean; it has not been reported from the western North Atlantic, but occurs in numbers off the northwest coast of Africa and near the Azores; small catches indicate its presence in the southwestern Indian Ocean from 5°S to 40°S latitude; isolated small-to-moderate catches south of Java, near the Marshall Islands, in the North Pacific, off California, and in the southeast Pacific

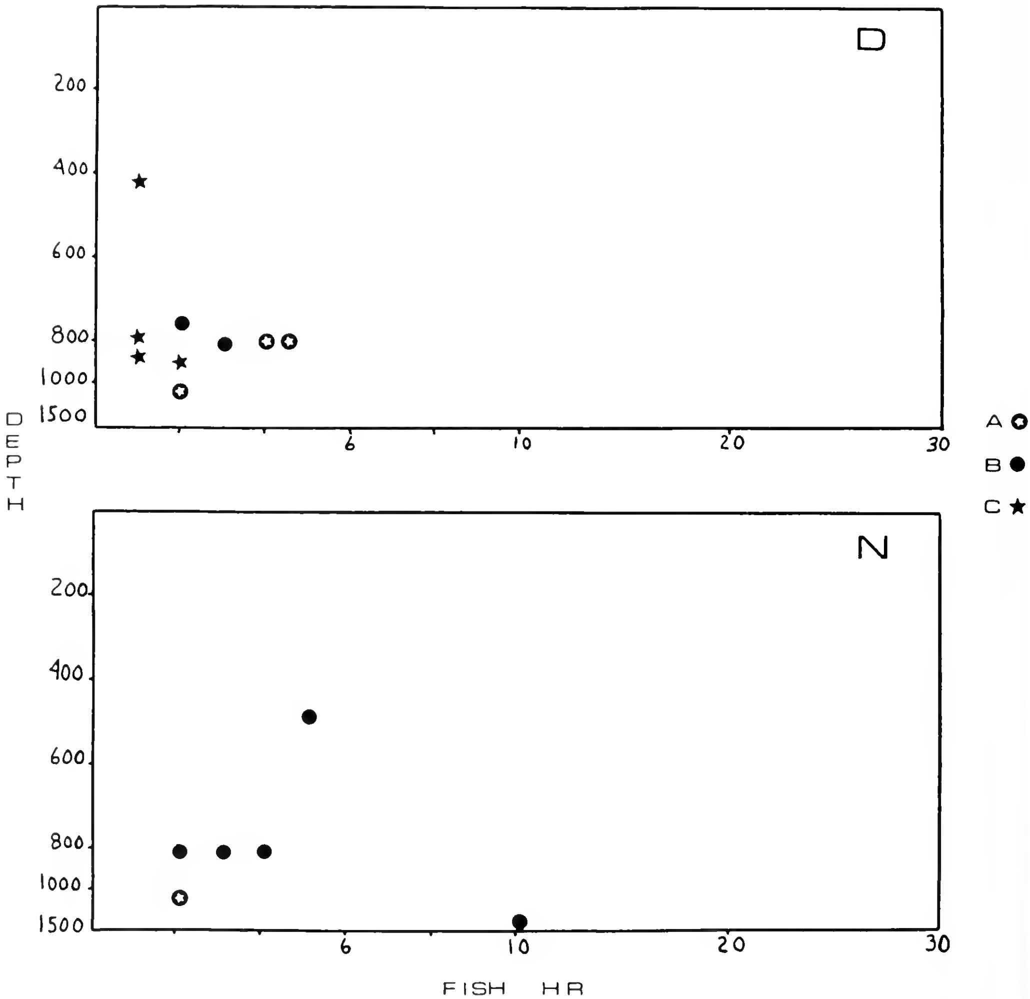


Figure 55. Diurnal vertical distribution of *S. pseudobscura* determined by rate of capture with depth during day (D) and night (N). A = Gulf of Guinea; B = NE Atlantic; C = Gulf of Mexico and Caribbean.

indicate a broad range in the Pacific which future collecting should better define.

Vertical distribution (Fig. 55): The deepest living species in the genus; data indicate a depth distribution from 500 m to 1500 m; greatest concentrations recorded occur between 800 m and 1500 m; overall small rates of capture plus relatively few deep stations may be indicative of a depth preference below 1000 m; no diurnal movement is indicated.

Geographic variation. Small sample sizes, few characters, and the few populations represented precluded a detailed examination of variability in this species. No differences were noted in the Atlantic populations, or in gill raker counts, or jaw length among all populations (Table 16, Fig. 56). The Indian Ocean population could be distinguished from the Atlantic ones by the supra-anal photophore measurement (Fig. 57).

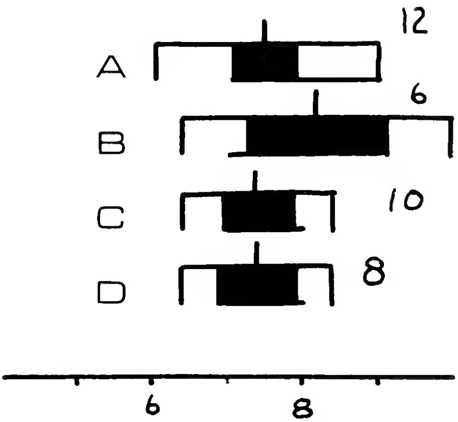


Figure 56. Geographic variation in gill roker count in S. *pseudobscura*. A = Caribbean; B = N Central Pacific; C = Indian Ocean; D = Marshall Islands. Numbers refer to sample size.

Sternoptyx diaphana Hermann
Figure 58

Sternoptyx diaphana Hermann, 1781: 33. In accordance with article 75a(i) Int. Code Zool. Nomen., a neotype is hereby designated: Neotype MCZ 46402; 11° 06′N, 78° 21′W; 8/7/66; R/V ANTON BRUUN, Cruise 19; Station 813. Cuvier and Valenciennes, 1849: 415; Günther, 1864: 387; Goode and Bean, 1896: 127; Alcock, 1896: 331; Gilbert, 1905: 601; Brauer, 1906: 69 (in part); 1908: 175 (eye muscles); Holt and Byrne, 1913: 20; Weber and DeBeaufort, 1913: 1; Jespersen, 1915: 12; Jespersen and Täning, 1919: 220 (eye); Borodin, 1931: 68; Jespersen, 1934: 15; Roxas, 1934: 287; Buen, 1935: 52; Fowler, 1936: 1208; Beebe, 1937: 22; Parr, 1937: 49; Norman, 1937: 82; 1939: 19; Nybelin, 1948: 25; Maul, 1949a: 17; 1949b: 13 (in part); Wilimovsky, 1951; Misra, 1952: 367; Koumans, 1953: 186; Mead and Taylor, 1953: 570; Smith, 1953: 102; Haig, 1955: 321; Rass, 1955: 328; Grey, 1959: 326; Koefoed, 1961: 11; Schultz, 1961: 617 (in part); 1964: 241 (in part); Backus et al., 1965: 139 (in part); Berry and Perkins, 1965: 682 (in part); Bussing, 1965: 185; Haedrich and Nielsen, 1966: 909; Bright and Pequegnat, 1969: 34.

Species distinction. See *S. obscura* (p. 69) and *S. pseudobscura* (p. 72).

Description. D. 9–11; A. 14–16; P. 10–11; total gill rakers 7–8 (9); vertebrae 29 (30).

Medium size species, seldom exceeds 55 mm SL; trunk very broad; its depth usually greater than its length; dorsal spine long, its length greater or equal to dorsal fin length; posterior anal pterygiophores short, little extension behind and on same level with anal photophores; supra-anal photophore low, not reaching more than one-half the distance from ventral body margin to midline, no body margin extension in front of anal photophores; jaws medium to small; teeth short and low; gill raker tooth plates with low spinate ridges; anterior dorsal

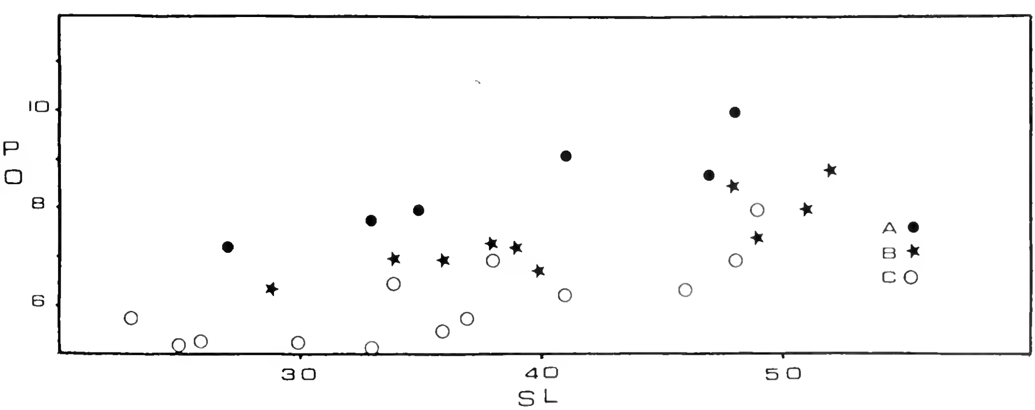


Figure 57. Geographic variation in distance from dorsal body margin of supra-anal photophore (PO) with standard length (SL) in S. *pseudobscura*. A = Indian Ocean; B = Gulf of Guinea; C = Gulf of Mexico and Caribbean.

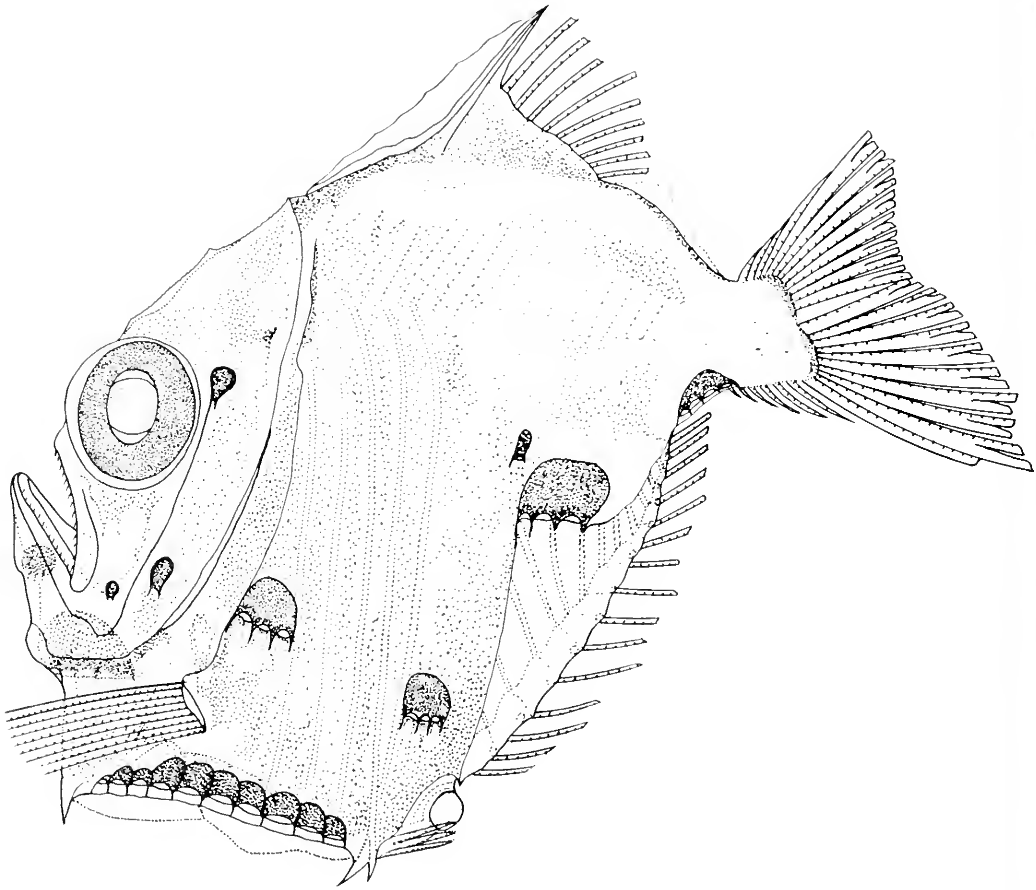


Figure 58. *Sternoptyx diaphana*; GALATHEA; Station 494; 33 mm.

surface of tongue with small nodules; postabdominal and anal pterygiophore spines usually shorter than others in genus; in preservative pigment dark dorsally, often light and dispersed in trunk region, usually little pigment present at base of caudal rays.

Neotype: measurements (mm): SL 28.4, BD 12.1, JL 05.3, CP 03.5, Ab. length 09.0; meristics: GR 7, D 10, A 15, anal photophores 3.

Distribution. Horizontal distribution (Fig. 59): Broadly distributed in the Atlantic, caught in moderate numbers in the South Atlantic off Brazil and from 20 W to the African coast at about 35 S; abundantly present in the Gulf of Guinea and the tropical Atlantic; taken abundantly in the southern Caribbean, the Gulf of Mexico, and straits of Florida; taken in the western North Atlantic; a large population occurs in the northeastern Atlantic from 25°N to 45°N latitude. In the western Indian Ocean small to moderate catches extend from 5°S to 35°S latitude, a single catch has been observed from the eastern Indian Ocean; numerous catches indicate this species present south of Java, near Borneo, and in the Banda Sea; known also between New Guinea and the Solomon Islands, it occurs in the western Pacific near the Philippines and along the coast of Japan, with a small

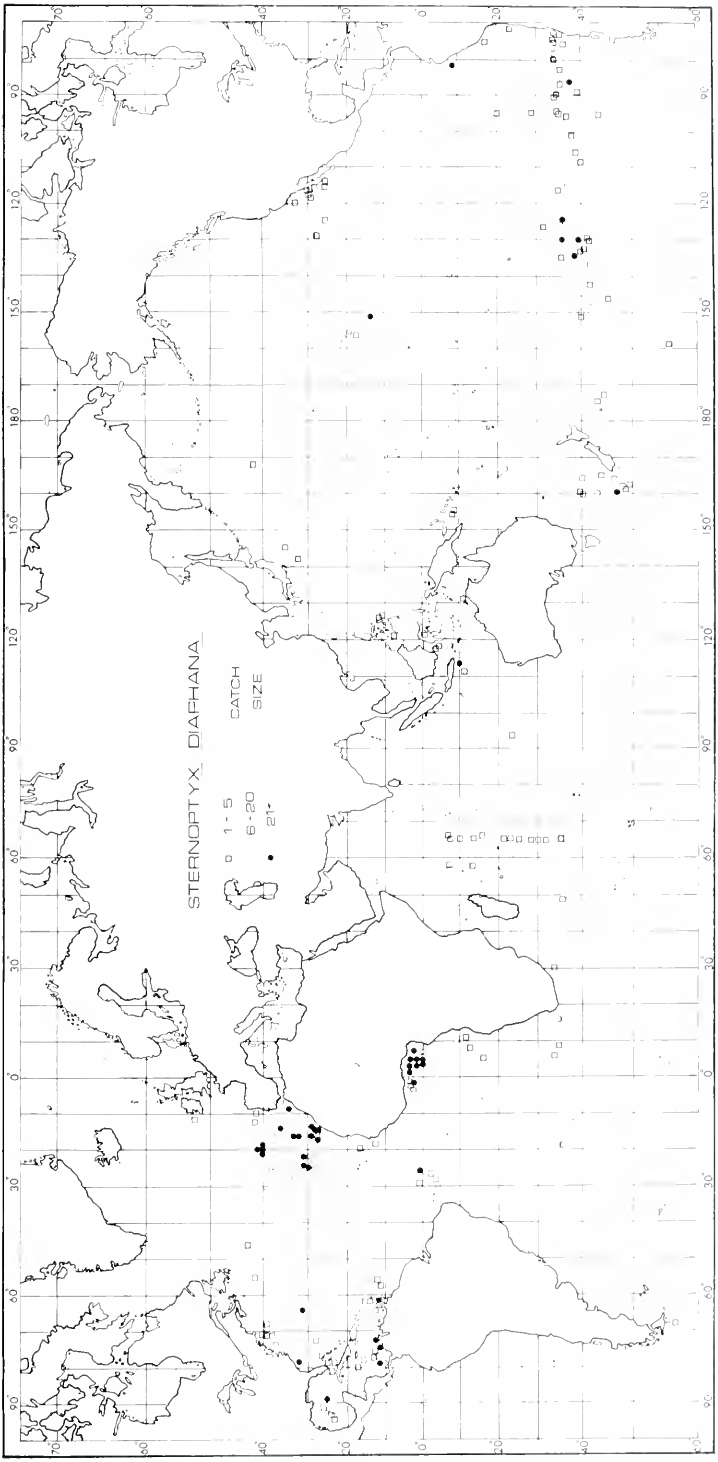


Figure 59. Horizontal distribution of *S. diaphana*. Catch size categories refer to the number of individuals taken in that haul.

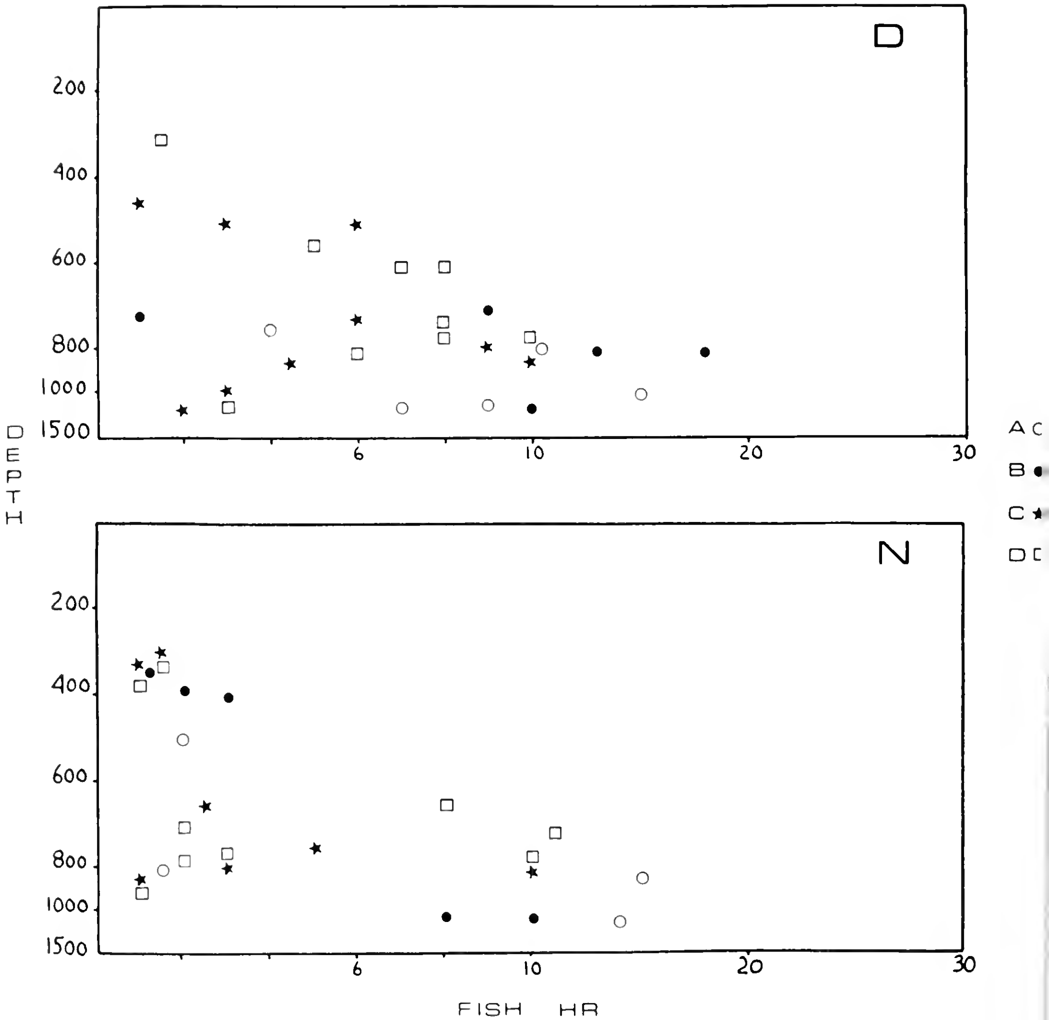


Figure 60. Diurnal vertical distribution of S. *diaphana* determined by rate of capture with depth during day (D) on night (N). A = Southern Ocean; B = Gulf of Guinea; C = Gulf of Mexico and Caribbean; D = NE Atlantic.

sample taken in the North Pacific; this species occurs in small numbers off lower California and has been reported abundantly southeast of Hawaii; a large population extends across the South Pacific from Chile to about 160°E longitude.

Vertical distribution (Fig. 60): Distributed between 400 m and 1200 m; major concentrations occur between 700 m and 900 m; no diurnal movement or marked geographical depth variation could be detected.

Geographic variation. With the exception of the Pacific southern ocean population, little geographic variation could be detected; characters were few and sample sizes small, however (Table 17, Fig. 61). The Southern Ocean population is quite distinct and certainly represents an instance of incipient speciation. Tables 17

'ABLE 17. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *S. DIAPHANA*.

Character	Regression A	Regression B
'aribbean		
aw length	−0.24	0.18 ± .066
hotophore	−2.04	0.37 ± .101
		N = 11
ava (10°S, 114°E)		
ody depth	−2.93	0.54 ± .107
bdominal length	0.78	0.31 ± .056
		N = 22
ndian Ocean (5°–40°S, 55°–65°E)		
ody depth	0.10	0.51 ± .095
bdominal length	1.18	0.31 ± .093
hotophore	0.20	0.29 ± .085
aw length	1.00	0.15 ± .088
		N = 12
outhern Ocean		
ody depth	−0.77	0.42 ± .044
bdominal length	1.18	0.31 ± 093
aw length	1.47	0.16 ± .041
hotophore	2.23	0.11 ± .033
		N = 40
outhern Ocean (Chile)		
ody depth	−1.50	0.41 ± .113
aw length	1.46	0.14 ± .037
		N =11

nd 18 indicate the degree of difference etween this population and others in the pecies. In body depth it falls somewhat etween most populations of *S. diaphana* nd *S. obscura* (Table 19). Phenotypically t has supra-anal photophore characteristics resembling some populations of *S. pseudobscura*. In most characters it falls closest to other populations of *S. diaphana*, especially in mouth and gill raker characteristics. Considering the lack of sympatry with other forms and the degree of distinctness between the species, it is presently considered to represent a distinct form of *S. diaphana*.

Genus *Polyipnus* Günther, 1887

Polyipnus Günther, 1887: 170 (type species: *Polyipnus spinosus* Günther, 1887, by monotypy).

Diagnosis. Ten abdominal, three supraabdominal, and a lateral photophore; post-temporal spine(s) well developed; a fused double dorsal pterygiophore forms short spines anterior to dorsal fin rays; cleithrum projects below pectoral fin forming fanlike, spine-bearing extension posteriorly; otoliths very large with characteristic armlike extension (see Kotthaus, 1967); three to four hypural elements in upper caudal lobe; lower jaw noticeably expanded dorsally.

Description. Photophores: PO 1; PTO 1; BR 6; I 6; PRO 1; SO 1; SP 3; SAB 3; AB 10; L 1; PAN 5; AN 6–14; SC 4.

Spines: Post-temporal extends posteriorly to form from one to three prominent spines; preopercle spined, the lateral surface often bearing spiny elements; retroarticular spined; ventral surface of lower jaw often serrate; cleithrum bears preabdominal spine; bony keel scales often bear spines ventrally; four postabdominal

'ABLE 18. SLOPE COMPARISONS BETWEEN REGRESSIONS OF SEVERAL CHARACTERS IN SPECIES OF *STERNOPTYX*. D = *S. DIAPHANA*; O = *S. OBSCURA*; P = *S. PSEUDOBSCURA*.

Character	Population 1	Population 2	T	P
3ody depth	Java D	Java O	2.780	.001
	Central Pacific P	Central Pacific O	2.362	.025
	Java D	Southern Ocean D	2.611	.010
bdominal length	Java D	Southern Ocean D	2.381	.023
'hotophore	Caribbean P	Caribbean D	4.977	.001
	Gulf of Guinea P	Caribbean D	3.240	.005
	Florida P	Caribbean D	2.767	.018

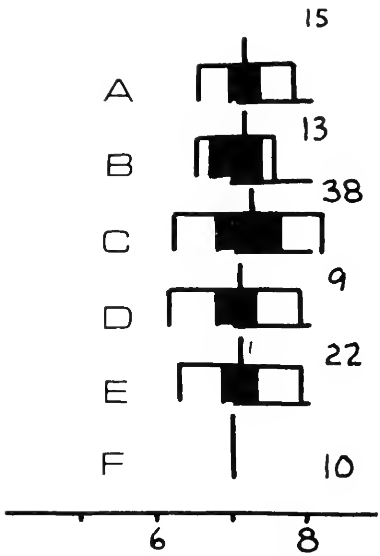


Figure 61. Geographic variation in gill raker count in *S. diaphana*. A = Caribbean; B = Indian Ocean; C = Southern Ocean; D = Pacific (Chile); E = Indian Ocean—S of Bali; F = Java Sea. Numbers refer to sample size.

spines; first anal pterygiophore may extend ventrally to form small spines.

Eyes: Large, well developed, nontelescopic, essentially laterally oriented.

Gill rakers: Number 10–28; well developed, long, often quite close together; first branchial arch considerably larger than succeeding arches; the inner surfaces of second and third cerato- and epibranchials bear tooth plates.

Jaws and dentition: Mouth small and vertically oriented; premaxilla long, toothed, and major upper jaw bone in gape; arm of first supramaxilla elongate; dorsal margin of lower jaw greatly expanded which, with broadening in the meso-and metapteryoid, make the mouth cavity a long conelike basket with a substantial distance between the mouth entrance and the beginning of the branchial arches; the maxilla is toothed, but essentially excluded from gape; teeth small to minute, no canines, vomer and palatines bear teeth.

Meristics: Vertebrae 31–36; C. 9+10; D. 10–17; A. 13–19.

Color: Bright silvery in life; dark dorsal pigment band often extends ventrally and may reach lateral midline; dark pigment may form lateral striated bands on posterior trunk.

Internal anatomy: Swim bladder and associated gland well developed, gland quite large, with grainy appearance; bladder thick walled, and often heavily invested with fatty tissue (see Marshall, 1960); digestive system simple with bipartate stomach, anterior section thick walled, the lining often raised into heavy

TABLE 19. COMPARISONS BETWEEN MEAN SLOPES OF SEVERAL CHARACTERS AMONG THE SPECIES OF *STERNOPTYX*. S.O. = SOUTHERN OCEAN POPULATIONS OF *S. DIAPHANA*; POP. # = NUMBER OF POPULATIONS; $\bar{x}$ SLOPE = UNWEIGHTED MEAN SLOPE; TOTAL # = TOTAL NUMBER OF FISH MEASURED OVER ALL POPULATIONS.

Species	Character	Pop. #	$\bar{x}$ Slope	Range	Total #
S. obscura	body depth	6	0.32	0.27–0.37	104
S. diaphana	body depth	2	0.525	0.51–0.54	34
S. diaphana (S.O.)	body depth	2	0.415	0.41–0.42	51
S. pseudobscura	body depth	1	0.49	0.49	13
S. diaphana	photophore	4	0.31	0.29–0.37	35
S. diaphana (S.O.)	photophore	1	0.11	0.11	40
S. pseudobscura	photophore	4	0.15	0.11–0.18	33
S. obscura	jaw length	4	0.13	0.09–0.15	56
S. diaphana	jaw length	5	0.196	0.15–0.23	41
S. diaphana (S.O.)	jaw length	2	0.15	0.14–0.16	51
S. pseudobscura	jaw length	5	0.15	0.15–0.16	46

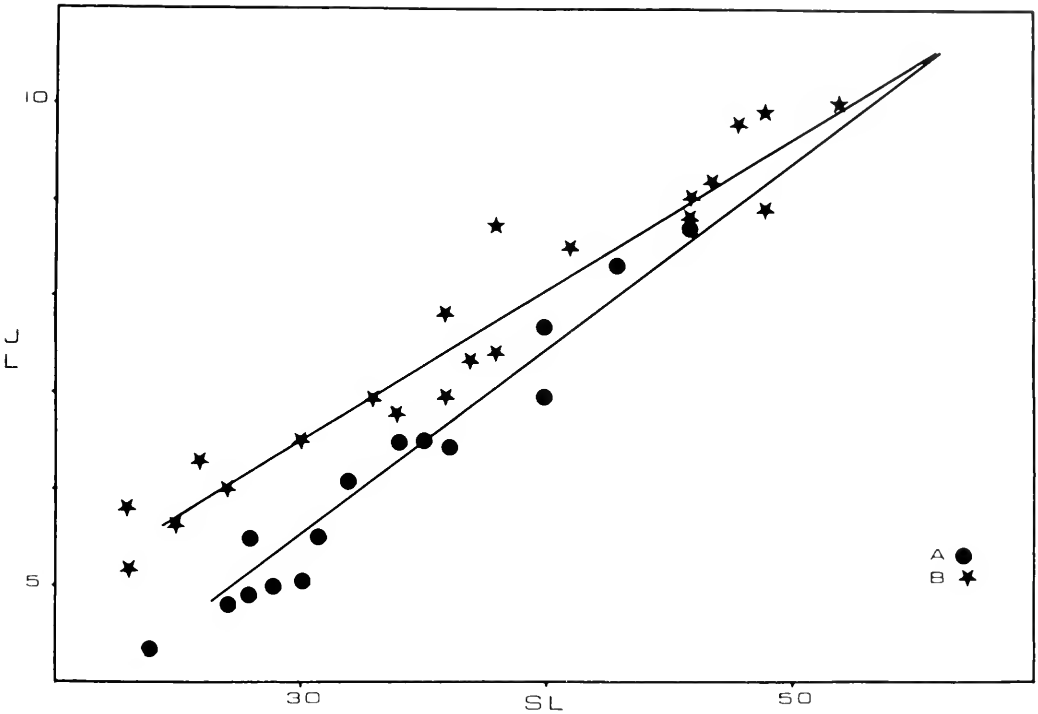


Figure 62. Regression of lower jaw length (JL) on standard length (SL) in *S. diaphana* (A) and *S. pseudobscura* (B) from the Tropical Atlantic.

ridged folds; the posterior section thin walled and extensible, six to ten pyloric caecae, short straight intestine, and a relatively large well-developed liver. Gonads, when mature, lie horizontally and laterally in the body cavity; cavity lined with pigmented membrane; nephritic tissue is not as well developed as in other genera.

Species complexes: As with *Argyropelecus,* there has been considerable radiation within the genus. There are three distinct species complexes, two closely related. The third complex, *P. spinosus,* is quite distinct. The latter appears more primitive in terms of axial and caudal skeleton characteristics. The *P. spinosus* complex differs from the other two groups as follows: greater development of the post-temporal spine complex; otoliths (Weitzman, personal conversation); four hypural elements in the upper caudal lobe; serrate lower jaw margin; spine-bearing abdominal keel plates; the second and third preterminal neural spines wedge shaped; extension of the cleithrum below the pectoral relatively more broadened; and the anal pterygiophore gap is reduced.

Within the *P. spinosus* complex there is a further dichotomy. *P. nuttingi, P. oluolus,* and *P. indicus* with peculiar reductions in post-temporal spine characteristics, form one group; *P. spinosus, P. sterope,* and *P. tridentifer* with a well-developed, post-temporal complex, form the other.

The *P. asteroides* and *P. laternatus* species complexes are more closely related. They differ primarily in post-temporal spine characteristics, body shape and size, photophore number and pattern, and dentition. Both complexes have similar otoliths and resemble each other osteologically.

The species *P. laternatus—P. omphus*

and *P. unispinus*—*P. aquavitus* form a dichotomy within the *P. laternatus* complex. The differences include preopercle spine length, body shape, photophore pattern, and some meristic differences (gill rakers, vertebral number).

P. asteroides—*P. polli*—*P. triphanos* and *P. matsubarai*—*P. meteori*—*P. kiwiensis*—*P. ruggeri* form a similar dichotomy within the *P. asteroides* complex. The latter group is characterized by an extremely long, narrow, posterior vomerine shaft, closely allied and fitting into the parasphenoid. This shaft bears teeth anteriorly, in addition to the normal lateral vomerine teeth. Other minor differences are also present.

Key to the Species of *Polyipnus*

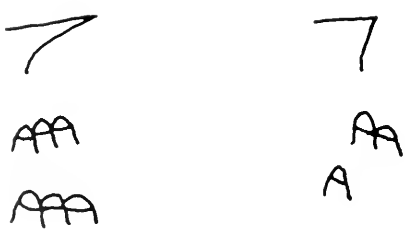
1a. Post-temporal spine complex, bearing one or two basal supplementary spines; dorso-lateral edge of fused, post-temporal-supracleithrum serrate; abdominal keel scales with spiny ventral surfaces; supra-anal photophore group usually not distinctly separated from anal group .... *P. spinosus* complex 3

b. Post-temporal spine simple, bearing no basal spines; lateral edge of post-temporal-supracleithrum smooth; keel scales with smooth ventral surfaces (except *P. unispinus*); supra-anal photophores separate, usually raised well above anal group 2

a. b.

2a. Post-temporal spine long, its length greater than one-fourth the diameter of orbit; anal photophore number 10 to 13 (adults only); body long and narrow, SL greater than 1.7 times body depth; first supra-anal photophore even with or raised above the second (except *P. laternatus* in which the first is slightly lower than the second) .... *P. laternatus* complex 8

b. Post-temporal spine short, its length less than one-fourth the diameter of orbit; anal photophore number 7 to 9 (occasionally 10); body more robust, SL less than 1.9 times body depth; first supra-anal photophore markedly lower than second .... *P. asteroides* complex 11



a. b.

3a. Post-temporal spine with two distinct basal spines; anal-subcaudal photophore distance less than one-third the length of the subcaudal group; anal photophore number 10 to 13 4

b. Post-temporal spine with a single distinct basal spine (this reduced in *P. oluolus*); anal-subcaudal distance greater than one-half of the length of the subcaudal group; anal photophore number 6 to 9 6

a.

b.

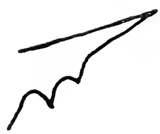
4a. Anal photophore number 10; SL less than 3.6 times body depth at end of dorsal fin; caudal peduncle broad, head length less than 2.8 times narrowest peduncle depth 5

b. Anal photophore number 12 to 13; SL greater than four times body depth at end of dorsal; caudal peduncle narrow, head length greater than three times narrowest peduncle depth .... *P. tridentifer* (p. 86).

5a. Post-temporal basal spines well developed, ventralmost basal spine length greater than one-half length of post-temporal spine; gill raker number 24–28 .... *P. sterope* (p. 88).

b. Post-temporal basal spines short, ventralmost basal spine less than one-fourth post-temporal spine length; total gill raker number 18 to 21 .... *P. spinosus* (p. 89).

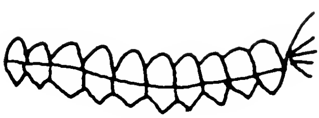
a.



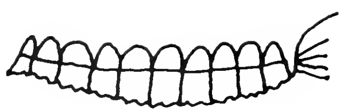
b.

6a. Abdominal keel scales triangulate, with one or two large ventral spines; post-temporal spine long, heavily spinose dorsally and laterally; first supra-anal photophore markedly lower than third; anal photophores 6 to 7 .... *P. oluolus* (p. 90).

b. Abdominal keel scales rectangular, with many small ventral spines; post-temporal spine long and smooth or short and spinose dorsally only; first supra-anal photophore about even with or raised above third; anal photophores 8 to 9 7



a.



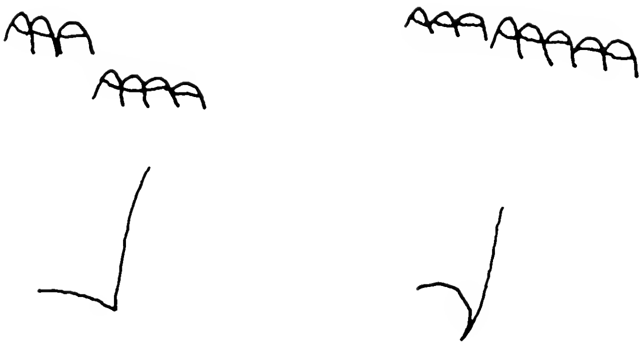
b.

7a. Ventral margin of subcaudal photophores with spines (adults); anal-subcaudal photophore distance less than three-fourths length of subcaudal group; first supra-anal photophore higher than the last; post-temporal spine long, greater than one-half diameter of orbit .... *P. indicus* (p. 91).

b. Ventral margin of subcaudal photophores smooth; anal-subcaudal distance greater than three-fourths length of subcaudal group; first supra-anal photophore lower than last; post-temporal spine short, less than one-half diameter of orbit .... *P. nuttingi* (p. 92).

8a. Gill rakers 18 to 21; supra-anal photophores distinctly raised above the anal group; preopercle spine short, somewhat triangulate 9

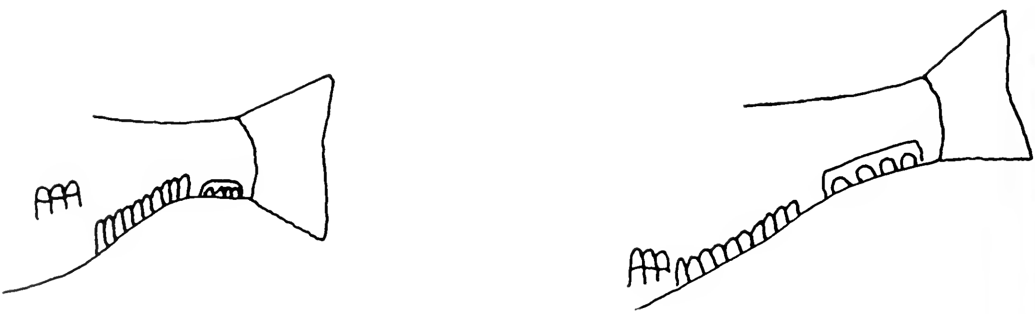
b. Gill rakers 12 to 14; supra-anal photophores not markedly raised above anal group; preopercle spine long and slender 10



a. b.

9a. Subcaudal photophores compact, length of subcaudal group less than narrowest caudal peduncle depth; distance from top of last supra-anal photophore to top of first anal greater than three-fourths length of preanal group .... *P. laternatus* (p. 92).

b. Subcaudal photophores somewhat spread; length of subcaudal group equal or greater than narrowest peduncle depth; distance from top of last supra-anal photophore to top of first anal less than one-half preanal length .... *P. omphus* (p. 94).



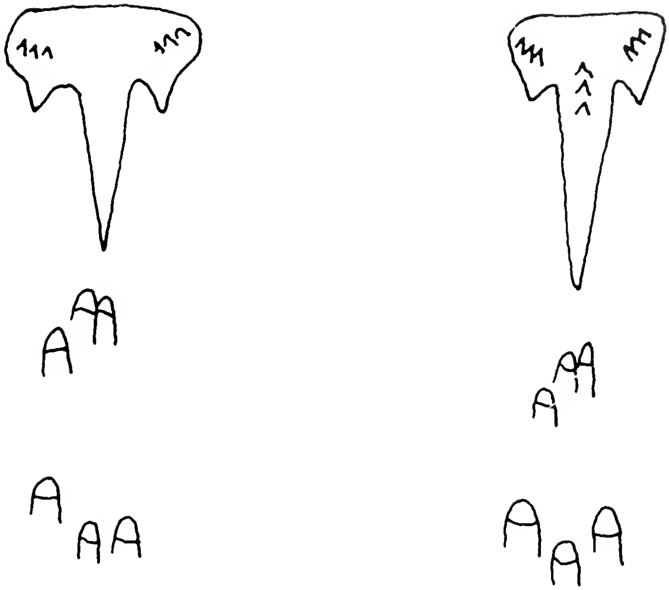
a. b.

10a. Posterior lateral margin of preopercle smooth; ventral keel scales smooth; dorsal spine short, length less than one-fourth diameter of orbit .... *P. aquaritus* (p. 96).

b. Posterior lateral margin of preopercle serrate; ventral edge of keel scales with small spinelets; dorsal spine long, length greater than one-half diameter of orbit .... *P. unispinus* (p. 97).

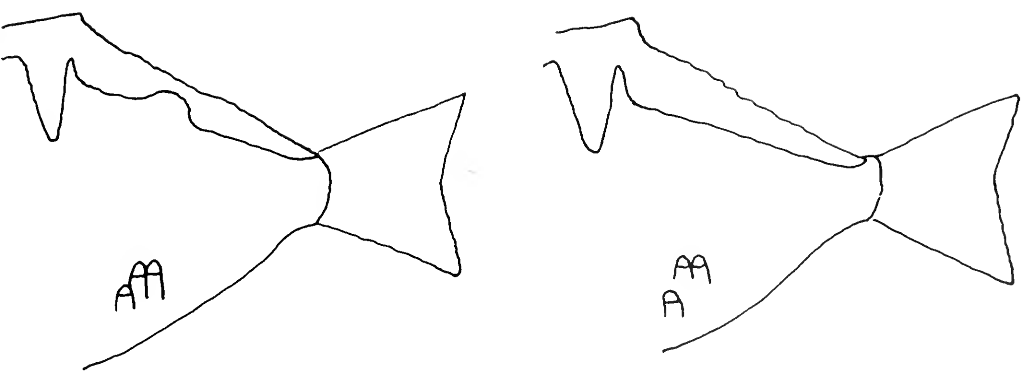
11a. Teeth absent on posterior vomerine shaft; second supra-anal photophore even with or raised above third; supra-abdominal photophores nonsymmetrical, first photophore raised well above other two 12

b. Teeth present on posterior vomerine shaft; second supra-anal photophore lower than third; supra-abdominal photophores symmetrical, first not markedly raised above third 14



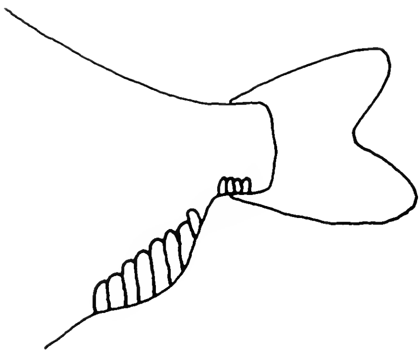
a. b.

12a. Gill rakers 16 to 18; dorsal rays 11 to 12; lower margin of dark dorsal pigment markedly raised above supra-anal photophores .... *P. triphanos* (p. 97).
b. Gill rakers 20 to 24; dorsal rays 14 to 16; lower margin of dark dorsal pigment straight from dorsal spine to caudal peduncle 13

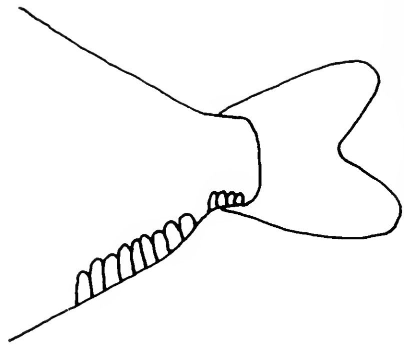


a. b.

13a. Anal pterygiophores form circular margin below anal photophores; anal photophores number 7 to 8; SL less than 3.5 times body depth at end of dorsal .... *P. polli* (p. 98).
b. Anal pterygiophore margin essentially straight; anal photophore number 9 (rarely 10); SL greater than 3.7 times body depth at end of dorsal .... *P. asteroides* (p. 99).



a.



b.

14a. Gill rakers 22 to 24; dark pigment bar extending to midline very narrow, its width less than greatest width of lateral photophore (see illustration p. 101) .... *P. matsubarai* (p. 101).

b. Gill rakers 13 to 18; dark pigment bar absent or much wider than width of lateral photophore 15

15a. Dark pigment bar greatly reduced or absent; supra-abdominal photophores essentially in straight line (see illustration p. 102); gill rakers 18 .... *P. ruggeri* (p. 102).

b. Dark pigment bar present, extending to midline; supra-abdominal photophores triangulate, the second markedly lower than the other two; gill rakers 13 to 17 16

16a. Gill rakers 13 to 15; light stripe behind dark pigment bar extends to mid-dorsal line; ventral border of dark dorsal pigment markedly raised above supra-anal photophores (taken from photo and description, Kotthaus, 1967) .... *P. meteori* (p. 104).

b. Gill rakers 16 to 17; light stripe behind dark pigment bar not extending to mid-dorsal line; ventral border of dark dorsal pigment not markedly raised above supra-anal photophores (see illustration p. 103) .... *P. kiwiensis* (p. 103).

Polyipnus tridentifer McCulloch
Figure 64

Polyipnus tridentifer McCulloch, 1914: 78 (lectotype AM E3543; designation Schultz, 1961; Australian Bight; not seen); Schultz, 1961: 619; 1964: 247.

Polyipnus spinosus: Weber and DeBeaufort, 1913: 1; Matsubara, 1950: 192; Okada and Suzuki, 1956: 297; Suzuki, 1964: 1.

Polyipnus frazeri Fowler, 1933: 257; Schultz, 1961: 620.

Species distinction. Differs from *P. spinosus* and *P. sterope* in its long, narrow trunk and caudal peduncle; long, smooth post-temporal spine; more sharply angled dorsal spine; multispinose subcaudal scales; less spinose abdominal keel scales; differs from *P. spinosus* by its much longer third basal post-temporal spine.

Description. D. 13–14; A. 15–17; P. (12) 13–14; total gill rakers (20) 21–24; vertebrae 33–34.

Medium size species, not often exceeding 60 mm SL; trunk tapering into long, narrow, caudal peduncle; its depth less or equal to length of subcaudal photophore group; post-temporal spine long, its length more than one-half the distance from its base to point of dorsal spine; second basal post-temporal spine long; dorsal surface of post-temporal spine relatively smooth, lacking marked serrations; supra-abdominal photophores arranged in steplike fashion, each raised an approximate equal distance above the next; abdominal keel scales spinose, although spines very short; scales below subcaudal photophores with several prominent spines; preopercle spine di-

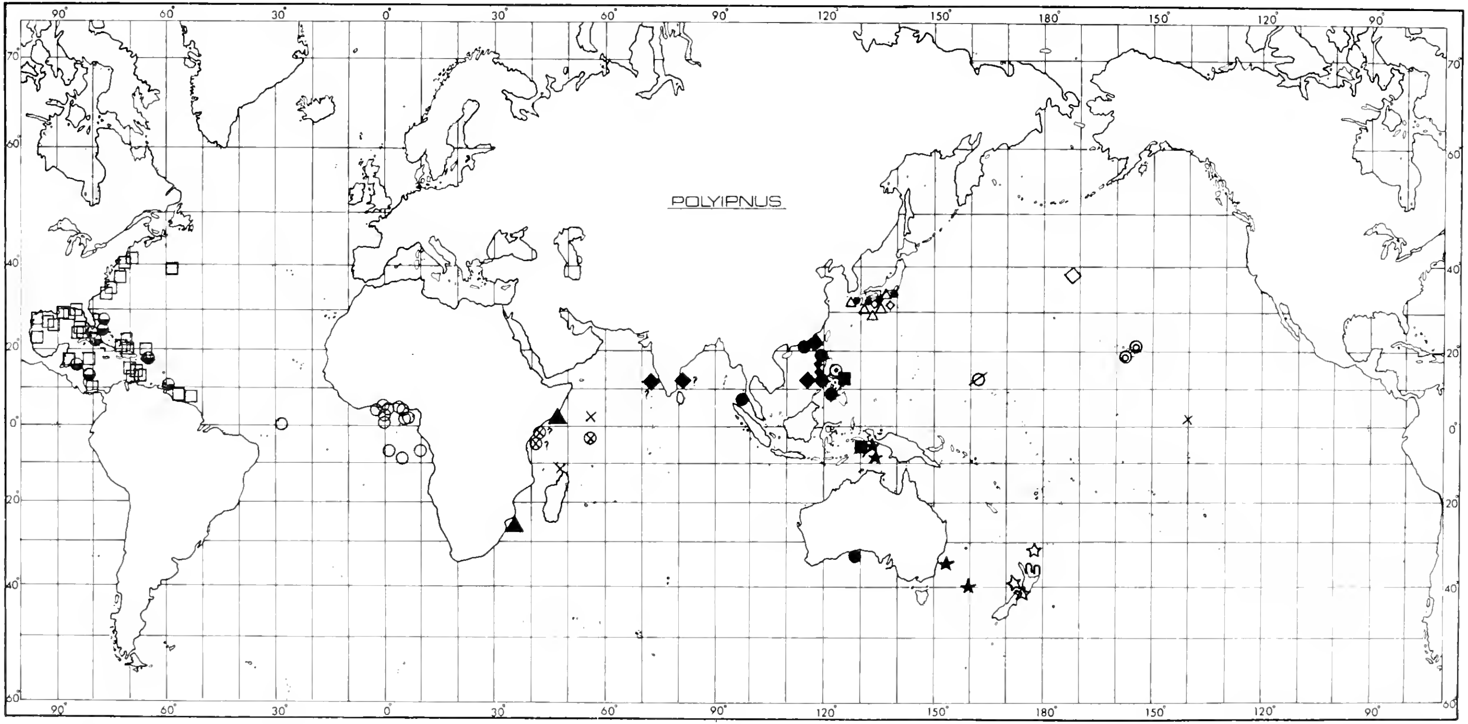


Figure 63. The distribution of the genus *Polyipnus*. Species: ◒ *P. laternatus*; □ *P. asteroides*; ○ *P. polli*; × *P. omphus*; ⊗ *P. meteori*; ▲ *P. indicus*; ◆ *P. spinosus*; ● *P. tridentifer*; ⊙ *P. triphanos*; ■ *P. unispinus*; ★ *P. aquavitus*; ☆ *P. ruggeri*; ∩ *P. kiwiensis*; △ *P. sterope*; ◇ *P. matsubarai*; ◎ *P. nuttingi*; ∅ *P. aluolus*.

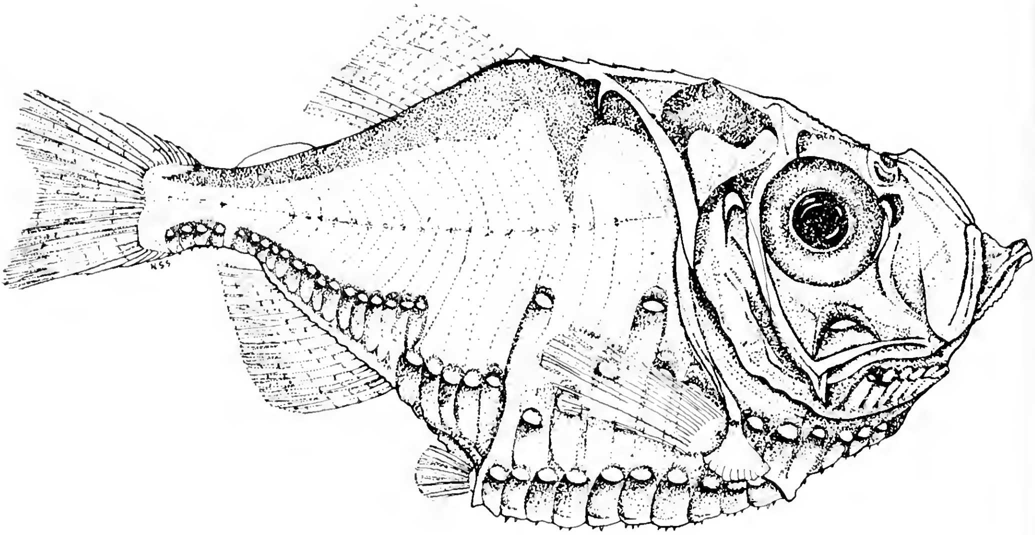


Figure 64. *Polyipnus tridentifer;* after Matsubara, 1950.

rected, at its base, posteriorly, curving distally to point ventrally or slightly anteriorly; jaws medium; teeth minute; gill rakers long; pigment in preservative dark dorsally with narrow, dark bar extending toward midline; pigment diffuse on trunk.

Distribution (Fig. 63). Restricted to the western Pacific, taken abundantly around the Philippines, off the south China coast, off Japan, in waters north of the Strait of Malacca, and in the Great Australian Bight.

Polyipnus sterope Jordan and Starks Figure 65

Polyipnus sterope Jordan and Starks, 1904: 581 (holotype USNM 51451; Sagami Bay, Japan; seen); Matsubara, 1941: 2; Haneda, 1952: 12 (light organs); Okada and Suzuki, 1956: 297; Suzuki, 1964: 1 (X-ray).

Polyipnus spinosus: Kamohara, 1952: 17.

Polyipnus spinosus sterope Schultz, 1961: 621; 1964: 247.

Species distinction. See *P. tridentifer*

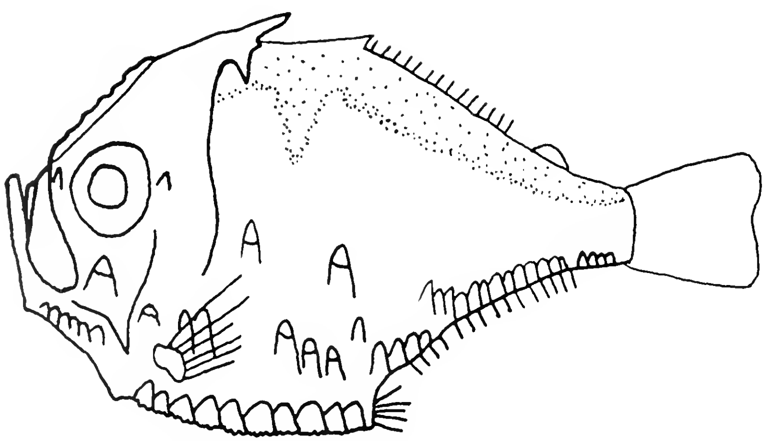


Figure 65. *Polyipnus sterope;* modified from Jordan and Starks, 1904.

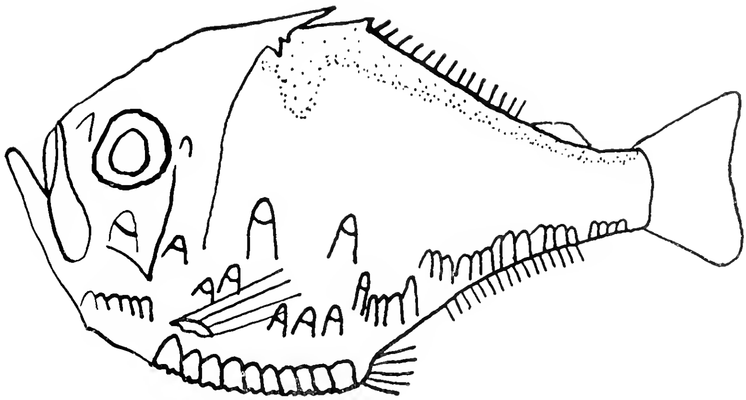


Figure 66. *Polyipnus spinosus*; modified from Günther, 1887.

(p. 86); differs from *P. spinosus* in its longer basal post-temporal spines; shorter preopercle spine; more raised first supra-abdominal photophore, somewhat shorter post-temporal spine in relation to its base-to-dorsal spine length, and higher gill raker count.

Description. D. 13–14; A. 15–17; P. 13–15; total gill rakers (23) 24–28; vertebrae 33–34.

Medium to large species, seldom exceeding 70 mm SL; trunk broadly tapering; caudal peduncle broad, its depth more than length of subcaudal photophore group; post-temporal spine spinose dorsally, its length substantially less than one-half distance from its base to point of dorsal spine; third basal post-temporal spine long, second basal spine prominent; dorsal spine high, with flangelike anterior portion not rising sharply from dorsal surface; supra-abdominal photophores positioned in a step-wise arrangement, with first photophore raised above other two; abdominal keel scales very spinose, including those ventral to preanal photophores; subcaudal scales either smooth or with single short spine; jaws medium; gill rakers long; preopercle spine curves slightly anteriorly; pigment in preservative dark dorsally with very narrow bar extending toward midline; pigment diffuse on trunk.

Distribution (Fig. 63). Known only from the waters around Japan, where it has been taken less abundantly than *P. tridentifer*.

Polyipnus spinosus Günther
Figure 66

Polyipnus spinosus Günther, 1887: 170 (holotype BMNH, East Indies; not seen); Alcock, 1896: 331; 1899: 135; Brauer, 1906: 69 (larvae, fig.) (in part); 1908: 175 (eye muscles); Roxas, 1934: 287; Misra, 1952: 367; Koumans, 1953: 186 (?); Samuel, 1963: 101 (?).

Polyipnus spinosus spinosus Schultz, 1961: 624; 1964: 247.

Species distinction. See *P. tridentifer* (p. 86) and *P. sterope* (p. 88).

Description. D. 13–14; A. 15–17; P. 13–15; total gill rakers 18–21; vertebrae 33–34.

Medium to small species, seldom exceeding 70 mm SL; trunk and caudal peduncle broad, its depth greater than or equal to length of subcaudal photophore group; post-temporal spine spinose dorsally, its basal spines reduced; post-temporal spine nearly equal to one-half the distance from its base to dorsal spine; dorsal spine similar to *P. sterope;* supra-abdominal photophore positioned with first photophore only slightly raised above other two; first two supra-anal photophores slightly raised from third; preopercle spine long, curving anteriorly; abdominal and preanal keel scales

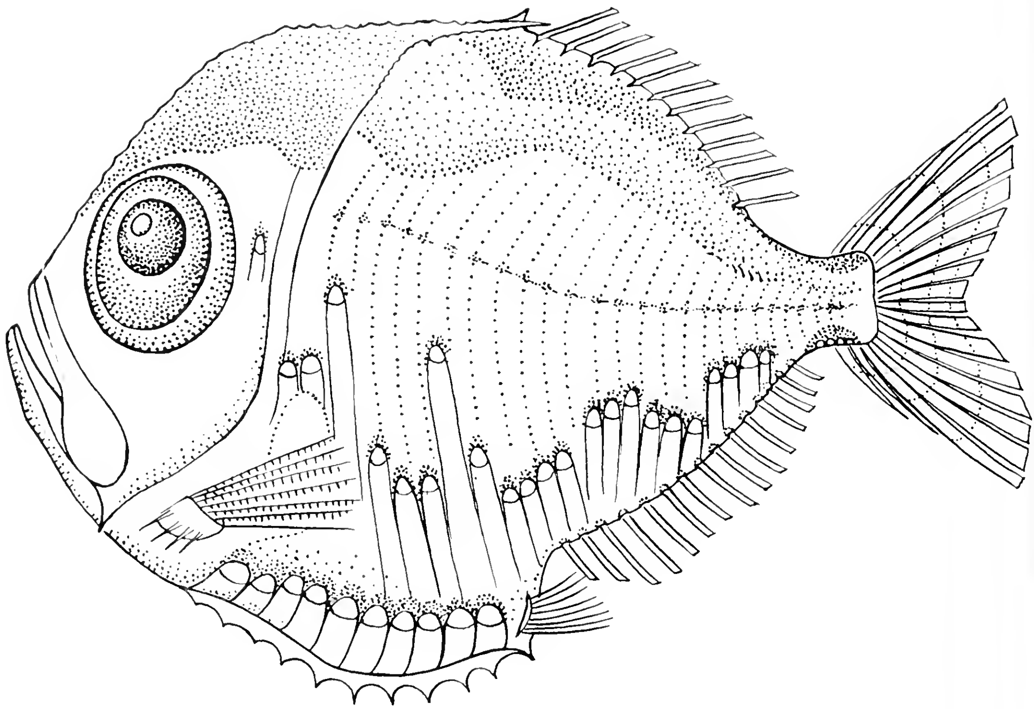


Figure 67. *Polyipnus oluolus*; R/V HUGH M. SMITH, Cruise 37; Station 43; SL 33 mm.

spinose; subcaudal scales with no spines to a single small spine; jaws medium; gill rakers long; pigment in preservative dark dorsally, with narrow dark bar extending toward midline; pigment less dark above anal photophores.

Distribution (Fig. 63). Taken in numbers off the Philippines and off the south China coast; reported from peninsular India, although these reports may represent *P. tridentifer*.

Polyipnus oluolus n. sp.

Figure 67

Holotype BCFH 2562; 11° 18′N, 162° 06′E; 12/9/56; R/V HUGH M. SMITH, cruise 37; Station 43.

Species distinction. Differs from *P. indicus* and *P. nuttingi* in its much broader body; post-temporal spine characteristics; triangular abdominal keel scales; supra-anal, supra-abdominal, and subcaudal photophore characteristics; and posterior extension of dorsal fin rays to end of anal photophores.

Description. D. 14; A. 15; P. 13; total gill rakers 19; vertebrae 33.

Known only from holotype, 33 mm SL; body very broad, narrowing abruptly to short narrow caudal peduncle; body depth 1.3 times into SL; post-temporal spine length more than one-half diameter of orbit, extends to origin of dorsal spine, very spinose dorsally and laterally; frontal ridges almost vertical, spinose; postabdominal spines well developed; abdominal keel scales extend well beyond ventral body margin; these scales sharply triangulate, coming to a single or double point ventrally; subcaudal scales smooth; first supra-abdominal photophore raised considerably above other two; subcaudal photophores raised well above anals; first supra-anal photophore noticeably lower than second

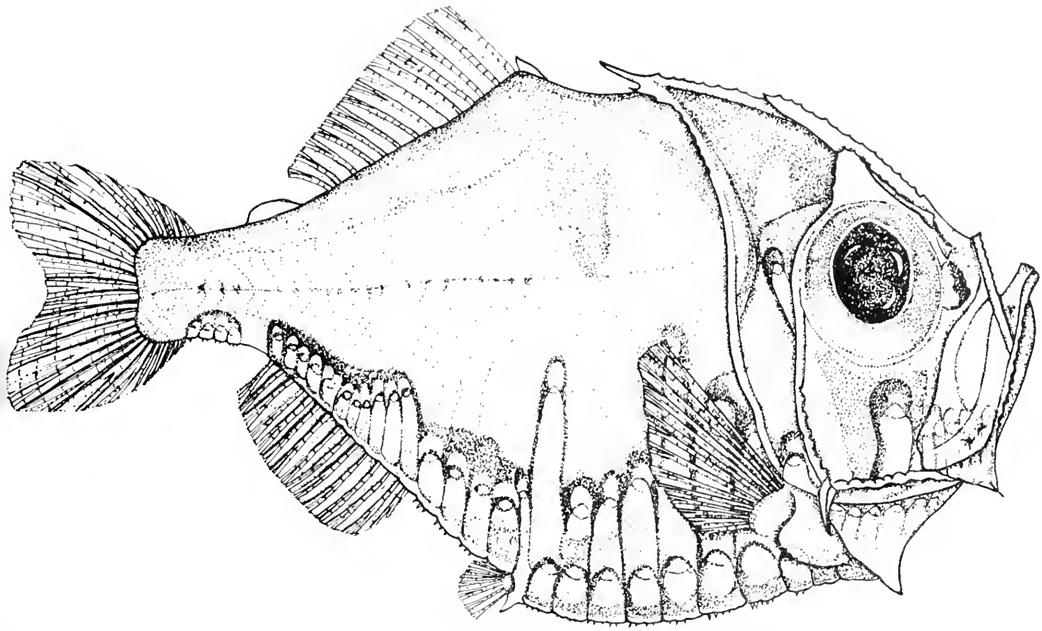


Figure 68. *Polyipnus indicus*; after Schultz, 1961.

which is lower than third; anal photophores in two distinct groups; jaws large; teeth small, several recurved ones in upper jaw; vomerine teeth well developed; gill rakers medium, spinose; in preservative pigment somewhat darker dorsally; pigment striations present on trunk.

Holotype: measurements (mm): SL 32.9, BD 25.7, JL 08.3, CP 03.9; meristics: GR 19, D 14, A 15, anal photophores 7; name: from the Hawaiian "oluolu," which means happy.

Distribution (Fig. 63). Known only from a single capture near the Marshall Islands.

Polyipnus indicus Schultz
Figure 68

Polyipnus indicus Schultz, 1961: 645 (holotype BMNH; off Zanzibar; not seen; paratype USNM 179897; seen); 1964: 241.
Polyipnus nuttingi: Norman, 1939: 20.

Species distinction. See *P. oluolus* (p. 90); differs from *P. nuttingi* by its longer, sharper post-temporal spines, less extended abdominal keel scales, less spinose ventral border of lower jaw, photophore characteristics, presence of spiny subcaudal keel scales, generally lower gill raker number, and shorter post-temporal base-to-dorsal spine length compared to post-temporal spine length.

Description. D. 13–14; A. 15–16 (17); P. (12) 13–14; total gill rakers 20–21 (22); vertebrae 33–34.

Largest specimen less than 55 mm SL; trunk tapering to long caudal peduncle; post-temporal spine long, thin, its length greater than one-half the diameter of orbit; basal post-temporal spine short; preopercle spine long, curving anteriorly; frontal ridges minutely spinose; abdominal keel scales do not extend much below ventral body margin, these scales with multiple spines; subcaudal scales spinose; supra-abdominal photophores in steplike arrangement with first photophore raised substantially above second; supra-anal photophores not well separated from anals; jaws large; teeth minute; underside of

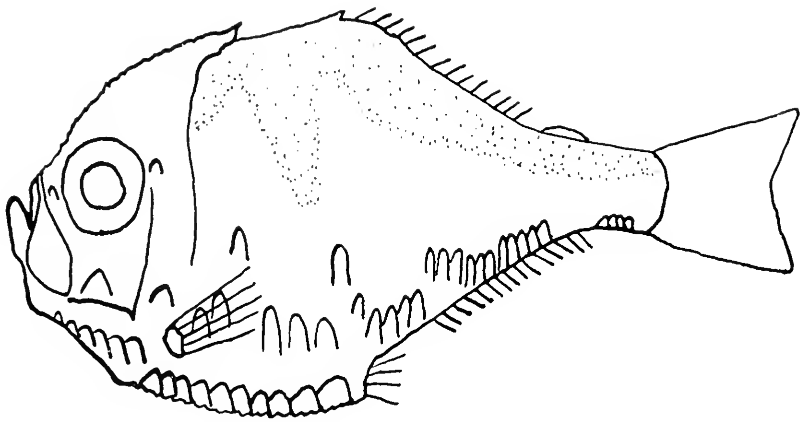


Figure 69. *Polyipnus nuttingi*; modified from Gilbert, 1905.

lower jaw smooth to slightly spinose; gill rakers short to medium with rough spinose internal surfaces; pigment in preservative dark dorsally and dark above anal photophores, dark pigment bar extends to midline; pigment in myomerelike striations on trunk, with definite pigment spots along posterior midline.

Distribution (Fig. 63). Known from three localities in the Indian Ocean along the east African coast from the equator to 30°S; reports of *P. spinosus* from this area may represent *P. indicus*.

Polyipnus nuttingi Gilbert
Figure 69

Polyipnus nuttingi Gilbert, 1905: 609 (holotype USNM 51599; Hawaii; seen); Fowler, 1949: 42; Haig, 1955: 321; Schultz, 1961: 640; 1964: 247.

Species distinction. See *P. oluolus* (p. 90) and *P. indicus* (p. 91).

Description. D. (12) 13–14; A. 15–16; P. 13–14; total gill rakers (21) 22–24; vertebrae 33–34.

Largest specimen less than 65 mm SL; body broad, tapering to long narrow caudal peduncle; post-temporal spine stout, relatively short (less than one-half eye diameter), slightly spinose dorsally; frontal ridges more vertically oriented than *P. indicus* and minutely spinose; preopercle spine short, curving anteriorly; abdominal keel scales with multiple spines; these scales extend well below ventral body margin; post-temporal spine length less than one-half the distance from its base to point of dorsal blade; subcaudal scales smooth; supra-abdominal photophores arranged in a straight line, steplike arrangement; the three supra-anal photophores separated slightly but definitely from anal photophore group; jaws large; teeth minute; undersurface of lower jaw markedly spinose; gill rakers long, spinose on internal surface; dorsal spine high; pigment in preservative similar to *P. indicus*, although dorsal pigment bar is longer and broader.

Distribution (Fig. 63). Known only from the Hawaiian Islands where it appears to be an endemic.

Polyipnus laternatus Garman
Figure 70

Polyipnus laternatus Garman, 1899: 238 (holotype MCZ 27945; off Barbados; seen); Parr, 1937: 49; Schultz, 1961: 639; 1964: 241.

Polyipnus spinosus: Brauer, 1906: 121 (in part); Goode and Bean, 1896: 127; Rivero, 1936: 50 (?).

Species distinction. Both *P. laternatus* and *P. omphus* differ from *P. aquavitus* and *P. unispinus* by their higher meristic

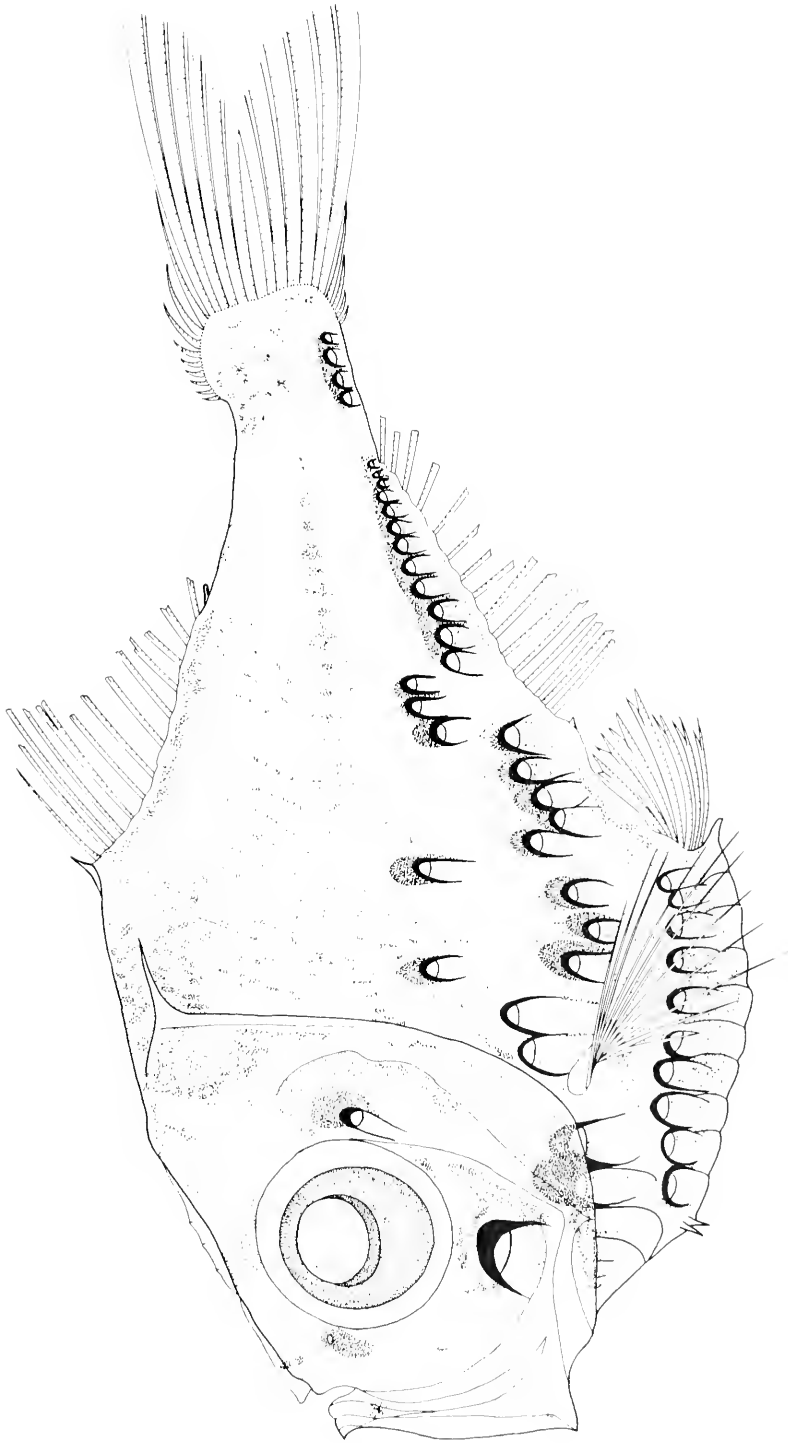


Figure 70. *Polyipnus laternatus*; R, V OREGON; Station 3609; SL 25 mm.

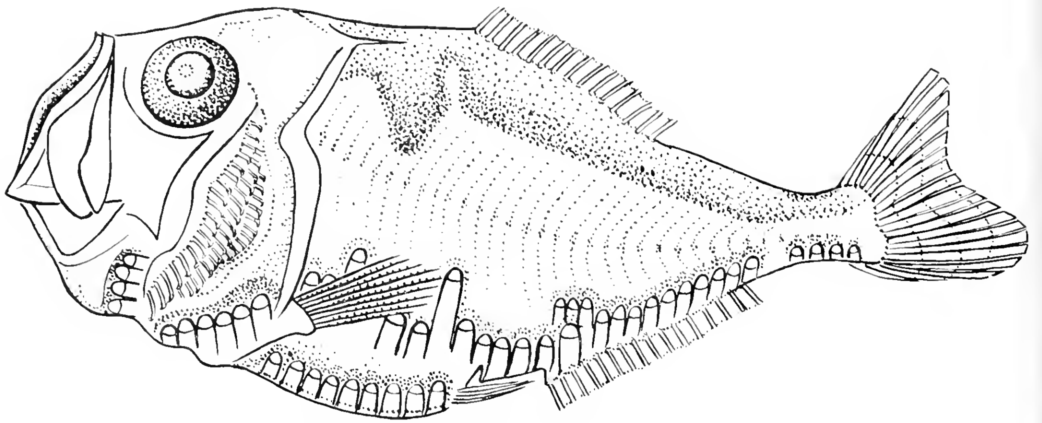


Figure 71. *Polyipnus omphus;* R/V DISCOVERY; Station 5509; SL 43 mm.

counts; shorter preopercle and dorsal spines; broader body, photophore and pigment characteristics. *P. laternatus* differs from *P. omphus* in its broader caudal peduncle; shorter, more compact subcaudal photophores, supra-anal and supra-abdominal photophore characteristics, slightly shorter preopercle spine, and relatively larger eye.

Description. D. 13–14 (15); A. (15) 16–17; P. 13–14; gill rakers (18) 19–22; vertebrae 32–33 (34).

Small to medium size species, rarely exceeding 55 mm SL; body relatively long and narrow, tapering into broad caudal peduncle, its width greater than width of subcaudal photophores; eye large, orbital diameter usually less than six times into SL; post-temporal spine long, thin, its total length variable (usually about one-half the diameter of orbit); dorsal spine short; preopercle spine short, broad, triangulate; abdominal keel scales smooth, not extended far beyond body margin; subcaudal photophores closely allied, little space between each photophore; supra-anal photophores raised well above anals, with first supra-anal slightly lower than second; first supra-abdominal photophore raised well above other two; second supra-abdominal even with or lower than third; jaws medium to small; teeth minute; vomerine and palatine teeth small but prominent; gill rakers long, spinose on inner surface; pigment in preservative dark dorsally, dark pigment bar usually does not reach midline; prominent, dark spots along trunk midline; myomerelike pigment striations dorsally and vertically from midline.

Distribution (Fig. 63). Restricted to the western Atlantic; abundant in the Caribbean off Venezuela and the central American coast, in the lesser Antilles, off Puerto Rico, Cuba, and in the straits of Florida; not reported from the Gulf of Mexico or the east coast of North America.

Polyipnus omphus n. sp.
Figure 71

Holotype BMNH: 11° 21'S, 48° 58'E; 8/21/64; R/V DISCOVERY; Station 5509.

Polyipnus laternatus: Kobayashi, 1963: 179; Kotthaus, 1967: 22 (otoliths, photo.).

Species distinction. See *P. laternatus* (p. 92). Both *P. laternatus* and *P. omphus* differ from *P. aquavitus* and *P. unispinus* by their higher meristic counts; shorter preopercle and dorsal spines; broader body, photopore and pigment characteristics. *P. laternatus* differs from *P. omphus* in its broader caudal peduncle; shorter, more compact subcaudal photophores; supra-anal and supra-abdominal photophore

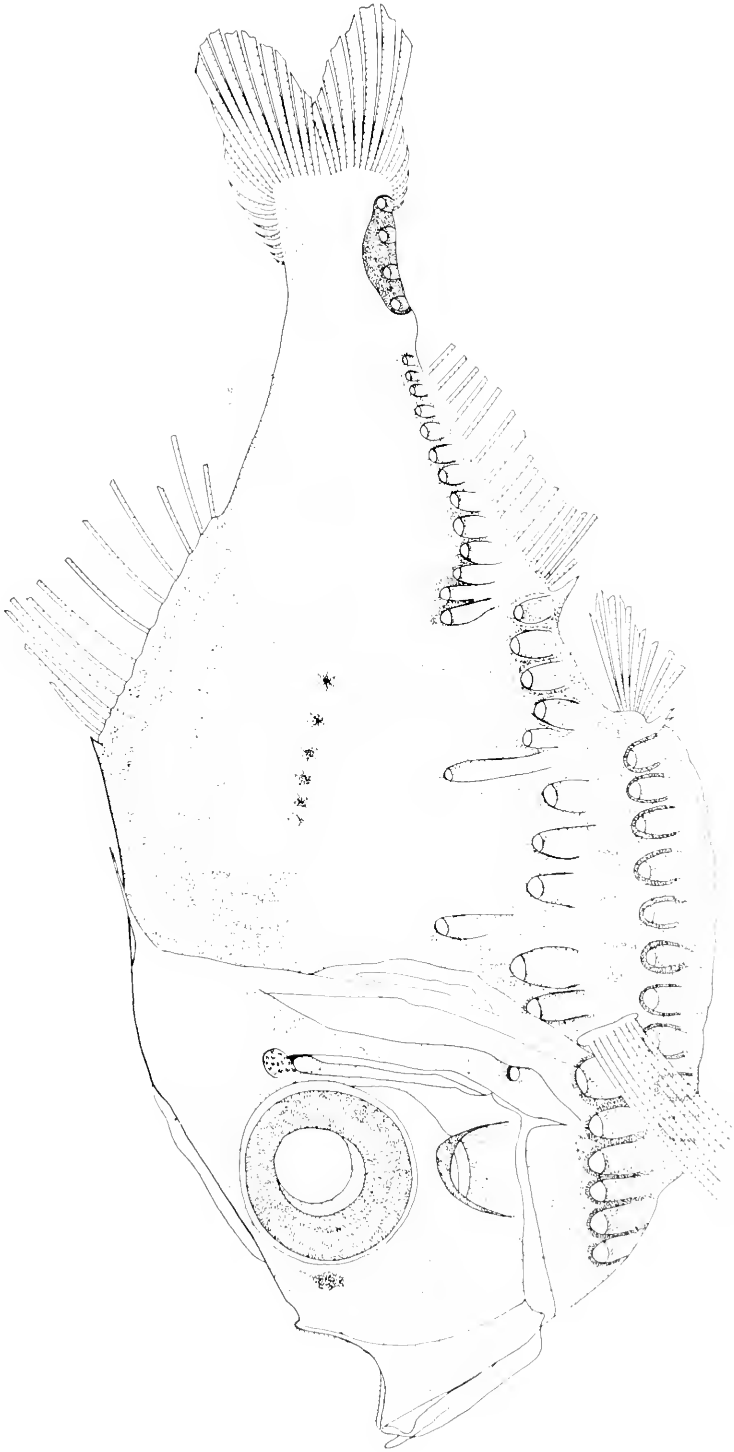


Figure 72. *Polyipnus aquavitus*; R/V GALATHEA; Station 551; SL 32 mm.

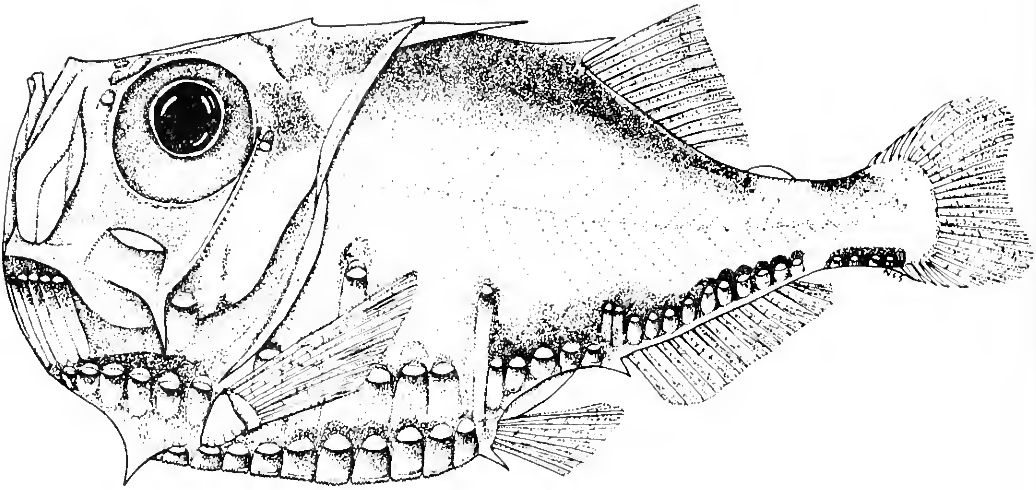


Figure 73. *Polyipnus unispinus;* after Schultz, 1938.

characteristics; slightly shorter preopercle spine; and relatively larger eye. The single specimen from the Pacific (SIO 60–236–101) appears slightly different phenotypically from the Indian Ocean forms. These two populations should be further examined when such material is available.

Description. D. 14–15; A. 16; P. 13–14; gill rakers 18–21; vertebrae (33).

Largest specimen less than 50 mm SL. body narrow, tapering into narrow caudal peduncle; its greatest depth less than length of subcaudal photophore group; eye relatively small, orbital diameter greater than six times into SL; post-temporal spine long, about one-half the diameter of orbit (or greater); dorsal spine short; preopercle spine short, narrowly triangulate; abdominal keel scales smooth, not extending far beyond body margins; subcaudal photophores spaced apart (about width of a photophore between them), distance between subcaudal and anal photophores about the same as length of one of the former; supra-anal raised only slightly above anals, with first supra-anal higher than second; supra-abdominal photophores in an oblique straight line; jaws medium; teeth minute; definite vomerine teeth present; gill rakers long, spinose; in preservative, pigment dark dorsally with broad, dark bar reaching to or near midline; dark pigment spots along trunk midline with pigment striations radiating from them; dark pigment above ventral photophores.

Holotype: measurements (mm): SL 40.1 BD 20.0, JL 06.1, CP 03.4; meristics: GR 19, D 14, A 16; anal photophores 11; name: from the Marathi word "omphus," roughly translated as "unwanted."

Distribution (Fig. 63). Extremely disjunct range; known from a few specimens north of Madagascar in the Indian Ocean and from a single capture in the Central Pacific north of the Marquesas Islands. Additional record: 00°00′, 165°42.5′W.

Polyipnus aquavitus n. sp.
Figure 72

Holotype ZMUC P20969; 33° 42′S, 151° 51′E 11/13/51; R/V GALATHEA; Station 551.

Species distinction. See *P. laternatus* (p. 92). *P. unispinus* differs from *P. aquavitus* by its longer dorsal and preopercle spines, spinose preopercle and ventral keel plates, shorter subcaudal to anal photophore distance, longer postabdominal and

anal pterygiophore spines, and its narrower trunk and caudal peduncle.

Description. D. (11) 12–13; A. 15–16; P. (12) 13–14; gill rakers 12–14; vertebrae (35).

Largest specimen less than 45 mm SL; body narrow, tapering into narrow caudal peduncle; its least depth less than length of subcaudal photophores; post-temporal spine long, length greater than one-half the diameter of orbit; dorsal spine short; preopercle spine short, sharp, length less than one-half the diameter of orbit; second preopercle spine reduced; lateral surface of preopercle smooth; abdominal keel scales smooth, not extended ventrally; supra-anal photophores only slightly raised from anals; first supra-anal photophore raised above second and third; anal-subcaudal photophore distance one-fourth or greater than length of latter; mouth small; teeth minute; gill rakers short to medium; in preservative, body pigment is dark over abdomen and trunk; pigment often present in band at base of caudal rays, few dark pigment spots along lateral midline.

Holotype: measurements (mm): SL 38.5, BD 17.7, JL 07.0, CP 03.6; meristics: GR 13, D 13, A 15, anal photophores 10; name: from the Danish national drink, akvavit.

Distribution (Fig. 63). Taken abundantly off Sidney, Australia, and known from single captures in the Banda Sea and between Tasmania and New Zealand.

Polyipnus unispinus Schultz
Figure 73

Polyipnus unispinus Schultz, 1938: 137 (holotype USNM 103153; Philippines; seen); 1961: 643; 1964: 247.

Species distinction. See *P. laternatus* (p. 92). Differs from *P. aquavitus* by its longer dorsal and preopercle spines, spinose preopercle and ventral keel scales, shorter subcaudal to anal photophore distance, longer postabdominal and anal pterygiophore spines, and its narrower trunk and caudal peduncle.

Description. D. 12–13 (14); A. 13–15; P. 12–13; gill rakers (11) 12–14; vertebrae (35–36).

Small, possibly a "dwarf" species, none yet exceeding 40 mm SL; body narrow, tapering into long narrow trunk and caudal peduncle; post-temporal spine long, almost equal to orbital diameter; dorsal spine long, high; its length about equal to one-half of orbital diameter; preopercle spine long, greater than one-half of orbital diameter; a well-developed second preopercle spine usually present; dorsal lateral surface of preopercle spinose; abdominal keel scales spinose ventrally; postabdominal and anal pterygiophore spines well developed; supra-anal photophores almost continuous with anals; first two supra-anals raised markedly above third; distance between subcaudal and anal photophores less or equal to one-fourth the length of the latter; mouth small; teeth minute; vomerine teeth prominent; gill rakers short to medium, well spaced; in preservative pigment slightly darker dorsally; abdomen and trunk relatively dark.

Distribution (Fig. 63). Taken in small numbers off the Philippines, and represented by two small samples from the Banda Sea.

Polyipnus triphanos Schultz
Figure 74

Polyipnus triphanos Schultz, 1938: 140 (holotype USNM 103027; Pescador Islands; seen); 1961: 640; 1964: 247.

Species distinction. See *P. asteroides* (p. 99); differs from *P. polli* by its higher anal photophore number, lower gill raker and dorsal ray counts, a straight ventral anal photophore margin, and the raised dorsal pigment border above the supra-anal photophores.

Description. D. 11–12; A. 17 (18, 19); P. 13–14; gill rakers (15) 16–18 (19); vertebrae (33).

Body broad, tapering into narrow caudal peduncle; its height slightly greater than length of subcaudal photophore group;

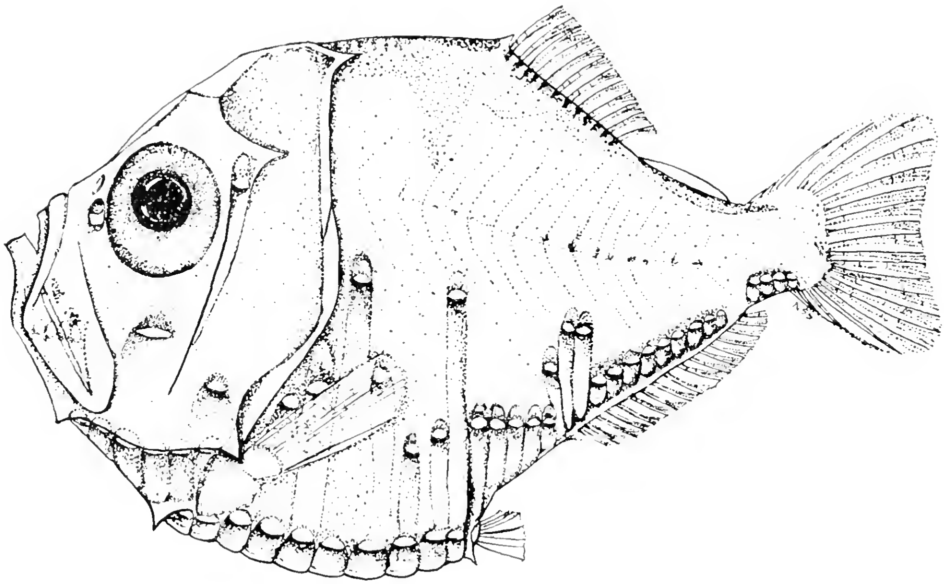


Figure 74. *Polyipnus triphanos;* after Schultz, 1938.

post-temporal spine short, needlelike; dorsal spine short; preopercle spine short, triangulate; abdominal keel scales extend only slightly below ventral body margin; first supra-anal photophore markedly lower than other two; first supra-abdominal raised above others, second lower than third, jaw medium to small; teeth minute; gill rakers medium, spinose; in preservative, pigment dark dorsally; dark pigment bar reaches almost to midline followed by light stripe reaching towards mid-dorsal line; ventral margin of dark dorsal pigment markedly raised on trunk above supra-anal photophores; pigment spots present on trunk midline, striations not distinct.

Distribution (Fig. 63). Known only from a few captures off the Philippines. Additional Record: 05° 01.0′S, 127° 57′E.

Polyipnus polli Schultz
Figure 75

Polyipnus polli Schultz 1961: 635 (holotype MRAC 93092; south east Atlantic; not seen, paratype USNM 179878; seen); 1964: 247; Blache, 1964: 71; Backus et al., 1965: 139.

Polyipnus laternatus: Norman, 1930: 305; Fowler, 1936: 1208; Poll, 1953: 65.

Polyipnus spinosus: Smith, 1953: 102 (?).

Species distinction. See *P. asteroides* (p. 99) and *P. triphanos* (p. 97).

Description. D. 14–15 (16); A. (15) 16–17; P. 13–14; gill rakers (20) 21–23; vertebrae 32–33.

Medium to small species, seldom exceeds 50 mm SL; body and trunk broad, narrowing abruptly to small, short caudal peduncle; post-temporal spines short, needlelike; dorsal spine short; preopercle spine short, triangulate; abdominal keel scales smooth; not extended ventrally; first supra-anal photophore lower than other two; first supra-abdominal raised well above second which is approximately even with third; subcaudal photophore group short, about equal to width of dorsal pigment bar at its center; body margin below anal photophores markedly curved; anal pterygiophores extend well beyond body margin; jaws small; teeth minute; gill rakers medium to long, and spinose; in preservative, pigment dark dorsally with pigment

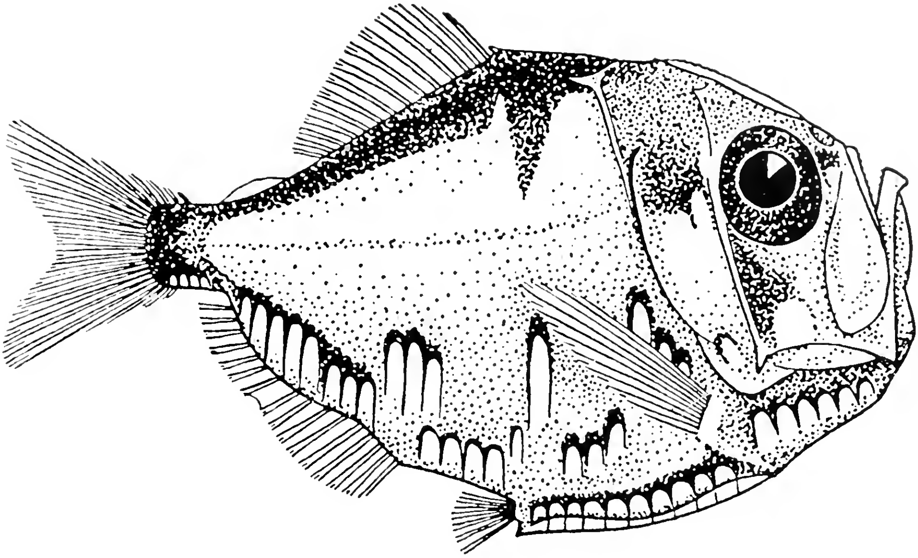


Figure 75. *Polyipnus polli;* after Norman, 1930.

bar reaching toward midline; ventral border of dorsal pigment in straight line, from lateral photophore to caudal peduncle; dark pigment spots on midline and between midline and border of darker dorsal pigment; pigment striations present on trunk.

Distribution (Fig. 63). Restricted to the southeastern Atlantic along the west African coast from the Gulf of Guinea to 10°S latitude.

Polyipnus asteroides Schultz
Figure 76

Polyipnus asteroides Schultz, 1938: 138 (holotype USNM; West Indies; not seen): 1961: 640; 1964: 247; Scott, 1965: 1303.
Polyipnus laternatus: Jespersen, 1934: 15.

Species distinction. P. asteroides, P. triphanos, and *P. polli* differ from *P. meteori, P. matsubarai, P. kiwiensis,* and *P. ruggeri* by their lack of teeth on the posterior vomerine shaft, and by supra-abdominal and supra-anal photophore characteristics; *P. asteroides* differs from *P. polli* by its greater number of anal photophores, less broad trunk, longer subcaudal photophore group, relatively straight anal photophore margin, and attainment of greater size; differs from *P. triphanos* by its less broad body, higher gill raker and dorsal ray counts, and body pigment characteristics.

Description. D. 14–16 (17); A. (15) 16–17 (18); P. (12) 13–14 (15); gill rakers 20–23 (24); vertebrae 32–33.

Large to giant species, often exceeds 70 mm SL; body relatively broad, tapering evenly to narrow but short caudal peduncle, its greatest depth greater than length of subcaudal photophores; posttemporal and dorsal spines short (less than one-fourth eye diameter); preopercle spine very short, triangulate; abdominal keel scales extend slightly below ventral body margin; first supra-anal photophore markedly lower than second; first supra-abdominal photophore raised well above other two, second and third supra-abdominals usually about same height; jaws medium to large; teeth minute; gill rakers medium to long, spinose on internal surface; in preservative, pigment dark dorsally; dark pigment bar extends toward but never

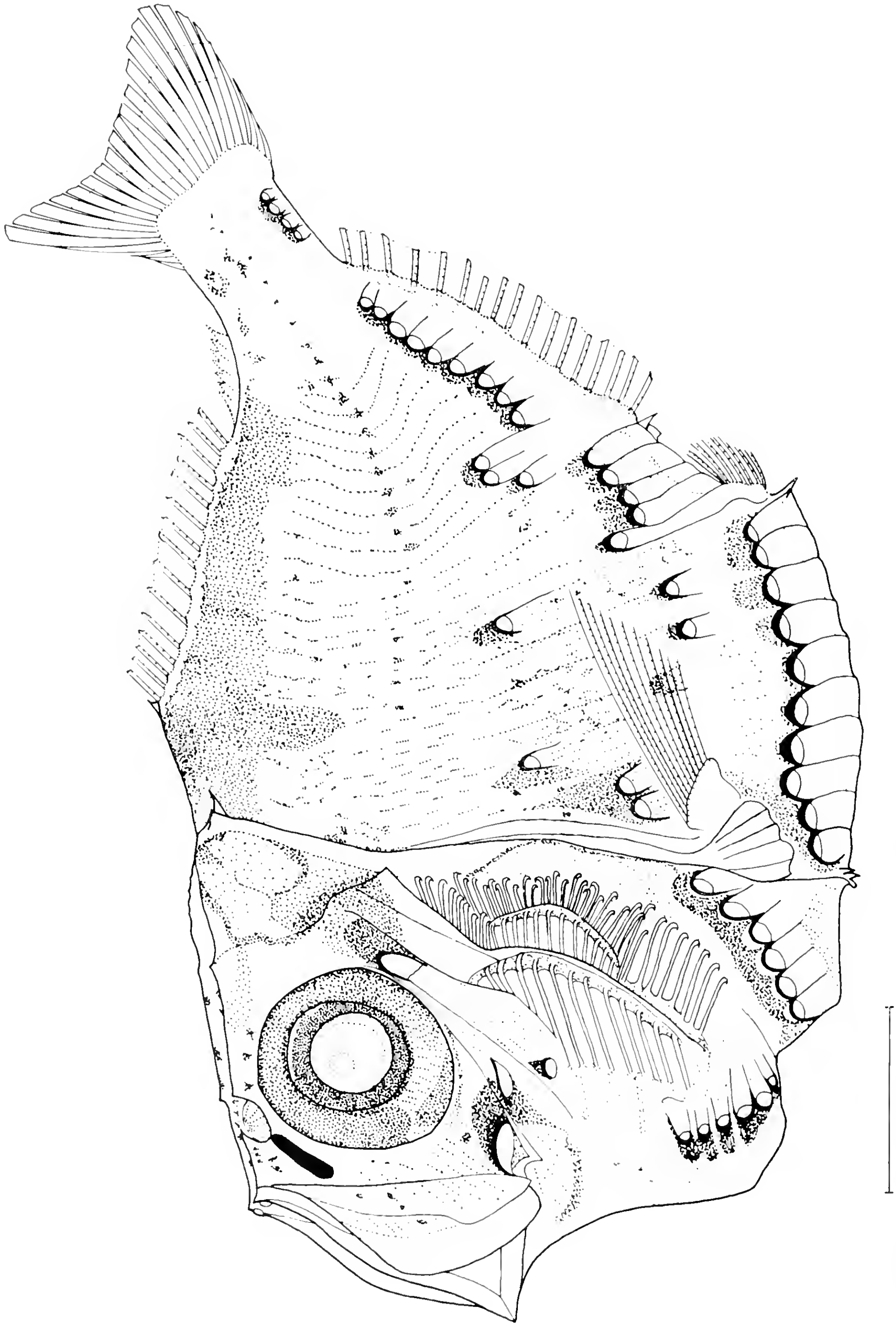


Figure 76. *Polyipnus asteroides*; R/V CHAIN, Cruise 60; Station 1295; SL 38 mm.

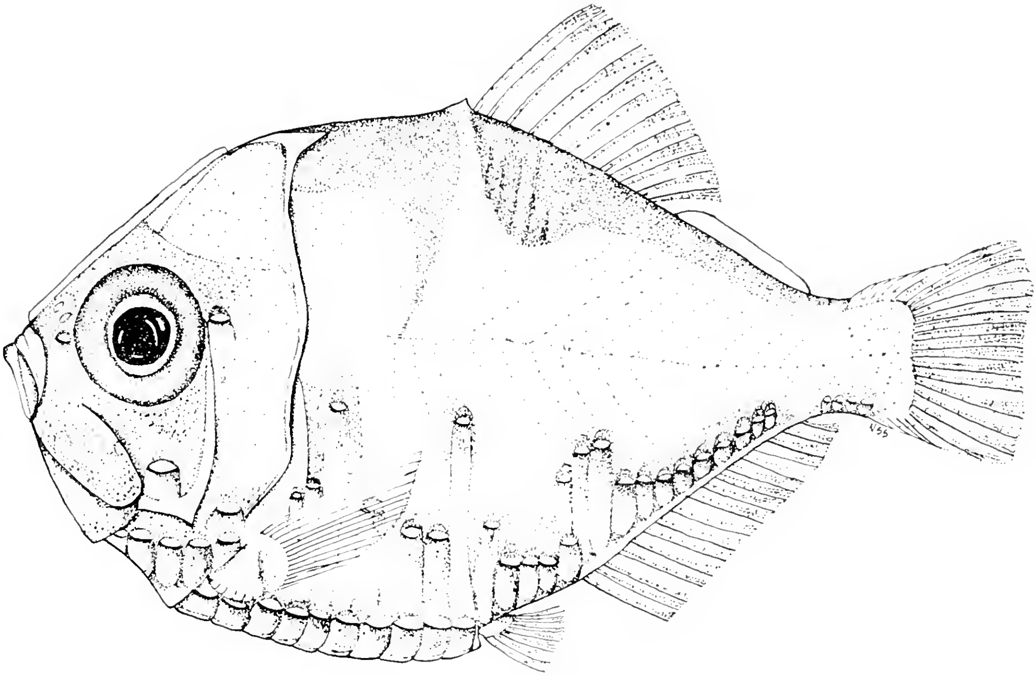


Figure 77. *Polyipnus matsubarai*; after Schultz, 1961.

reaches midline; lateral border of dark dorsal pigment straight from dorsal spine to caudal peduncle; dark pigment spots mark lateral midline, pigment striations present on trunk.

Distribution (Fig. 63). Restricted to the western North Atlantic; abundant in the Caribbean and Gulf of Mexico from the coast of Venezuela to the straits of Florida; occurs off the outer islands of the West Indies and less abundantly along the east coast of North America; a single capture has been reported as far north as the Gulf of Maine.

Polyipnus matsubarai Schultz
Figure 77

Polyipnus matsubarai Schultz, 1961: 641 (holotype USNM 179793; Kumanonada, Japan; seen); 1964: 247.
Polyipnus japonicus Schultz, 1961: 643; 1964: 247.
Polyipnus asteroides: Matsubara, 1941: 2; 1950: 192.

Species distinction. See *P. asteroides* (p. 99); differs from *P. ruggeri*, *P. kiwiensis*, and *P. meteori* by its higher gill raker count, long narrow caudal peduncle, and very narrow dorsal pigment bar.

Description. D. 12 (13); A. 16–17; P. (12) (13) 14–16; gill rakers 22–24; vertebrae 33.

Largest specimens have not exceeded 50 mm SL; body broad, tapering into long, relatively narrow caudal peduncle; its length equal to or greater than its greatest depth; post-temporal spine rather long and needlelike, its length about one-fourth the orbital diameter; dorsal spine short; preopercle spine short, triangulate; abdominal keel scales smooth, with no ventral extension; first supra-abdominal photophore raised above second which is equal to or slightly raised above third; supra-anal photophores in steplike arrangement, the third being highest; first three anal photophores even and parallel to midline; jaws

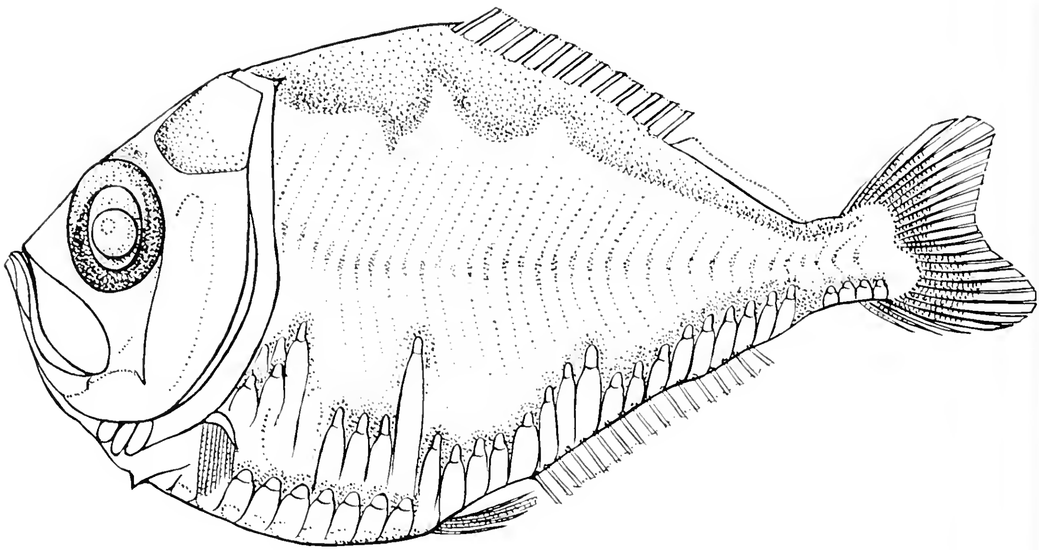


Figure 78. *Polyipnus ruggeri*; R/V TUI; New Zealand; SL 47 mm.

medium; teeth present on long posterior shaft of vomer lying ventral to parasphenoid, resulting in three distinct tooth bearing areas on the vomer; gill rakers medium; in preservative, dorsal pigment bar is extremely narrow and reaches to midline; dorsal pigment border is broken by light stripe behind pigment bar, reaching broadly to mid-dorsal line; dorsal pigment border raised slightly above supra-anal photophores; small, dark pigment spots mark lateral midline.

Distribution (Fig. 63). Abundant in the waters off Japan in the North Pacific; a single capture in the mid-North Pacific represents this species.

Polyipnus ruggeri n. sp.
Figure 78

Holotype DMNZ 4670; 31° 57′S, 177° 38′E; 7/24/62; R/V TUI.

Species distinction. Differs from the *P. asteroides* (p. 99) group by dentition and photophore characteristics and from *P. matsubarai* (p. 101) by dorsal pigment and gill raker characteristics; differs from *P. meteori* and *P. kiwiensis* by its dorsal pigment characteristics, higher gill raker count, and photophore patterns; further differs from *P. kiwiensis* by its smaller, rounder eye, longer, narrower caudal peduncle, and lesser distance between frontal crests (interorbital).

Description. D. 12; A. 16–17; P. 15; gill rakers 18; vertebrae (33).

Largest specimen less than 60 mm SL; body broad, tapering into somewhat long and narrow caudal peduncle; its length greater than depth; post-temporal spine short, rough surfaced dorsally, less than one-fourth of the diameter of orbit; dorsal spine short, low; preopercle spine triangulate; eye large, round, its length about equal to width; greatest distance between frontal crests (interorbital) less than or equal to length of subcaudal photophore group; abdominal keel scales not extended ventrally; supra-abdominal photophores in essentially straight line, first may be slightly raised above third; first supra-anal photophore noticeably lower than second, which is lower than third; jaws medium to large; teeth present on posterior vomerine shaft; gill rakers medium, slightly spinose; in preservative, pigment dark dorsally with a

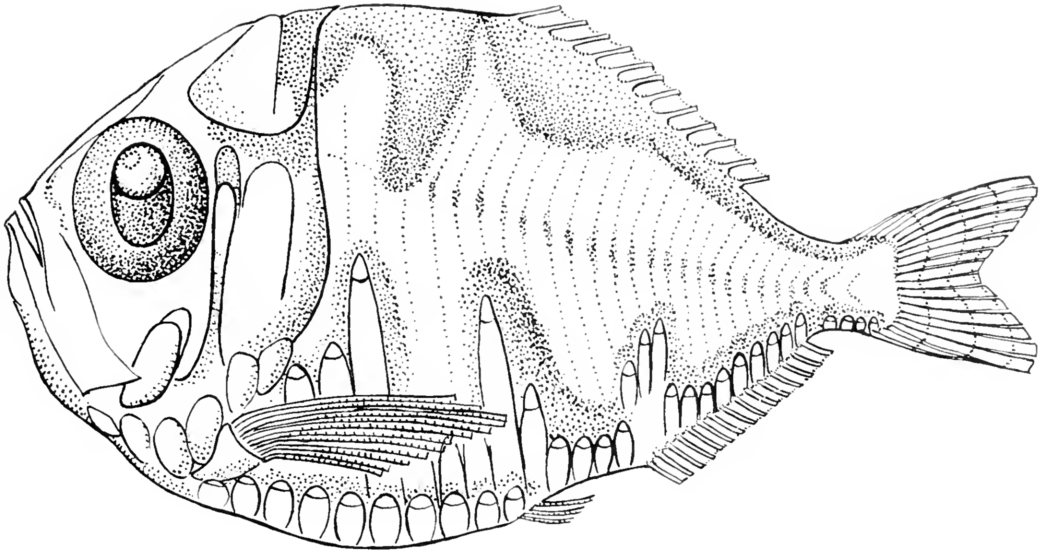


Figure 79. *Polyipnus kiwiensis;* R/V TUI; New Zealand; SL 60 mm.

very reduced pigment bar; much reduced light stripe behind bar does not reach mid-dorsal line; ventral border of dorsal pigment raised above supra-anal photophores; small dark pigment spots present on lateral midline.

Holotype: measurements (mm): SL 46.8, BD 30.3, JL 09.7, CP 05.5; meristics: GR 18, D 12, A 17; anal photophores 9; name: named in honor of New Zealand's national sport, rugby.

Distribution (Fig. 63). Known only from a few small captures off Wellington, New Zealand, and west of the Kermadec Islands.

Polyipnus kiwiensis n. sp.
Figure 79

Holotype DMNZ 4802; 36° 50′S, 176° 10′E; 9/26/62; R/V TUI.

Species distinction. Differs from *P. asteroides* (p. 99) group by photophore characteristics and teeth on posterior vomerine shaft; from *P. matsubarai* by gill raker number and dorsal pigment characteristics (*P. matsubarai*, p. 101); from *P. ruggeri* (p. 102) by dorsal pigment characteristics, eye size, gill raker number, caudal peduncle, and interorbital crests; differs from *P. meteori* by its higher gill raker counts, larger eye and mouth, photophore and dorsal pigment characteristics.

Description. D. (11) 12; A. 16–17; P. 15–16; gill rakers 16–17; vertebrae (32) 33 (34).

Largest specimens less than 70 mm SL; body broad, tapering rather abruptly into short caudal peduncle; its depth about equal to its length; post-temporal spine short, less than one-fourth the diameter of orbit; dorsal spine short, preopercle spine triangulate; eyes extremely large, their diameter less than seven times into SL; greatest distance between frontal crests (interorbital), greater than length of subcaudal photophore group; abdominal keel scales not extended ventrally; first and third supra-abdominal photophores about even and raised well above second; first supra-anal photophore noticeably lower than second, which is slightly lower than third; jaws large, broad; teeth well developed on posterior vomerine shaft and lower jaw; gill rakers medium; in preservative broad, dark, dorsal bar reaches to midline; light stripe posterior to dorsal

bar not reaching to mid-dorsal line; ventral border of dark dorsal pigment only slightly raised above supra-anal photophores; small dark pigment spots on lateral midline.

Holotype: measurements (mm): SL 59.5, BD 36.4, JL 14.3, CP 09.7; meristics: GR 17, D. 12, A. 17; anal photophores 10; name: from Kiwi—a New Zealand bird; in the vernacular, a Kiwi is a native of New Zealand.

Distribution (Fig. 63). Taken in moderate numbers near Red Mercury Island off the northeastern coast of North Island, New Zealand.

Polyipnus meteori Kotthaus

Polyipnus meteori Kotthaus, 1967: 27 (holotype IOES 20; off Seychelles, Indian Ocean; not seen).

Species distinction. See *P. asteroides* (p. 99), *P. matsubarai* (p. 101), *P. ruggeri* (p. 101), and *P. kiwiensis* (p. 103).

Description. (From description of holotype (Kotthaus, 1967) and photograph.) D. 12; A. 16; P. 15; gill raker number 13–15.

Known only from holotype (SL 37 mm); body broad, tapering to relatively long caudal peduncle (appears shorter than *P. matsubarai*); post-temporal spine needle-like, about equal to one-fourth the eye diameter; dorsal spine short; abdominal keel scales smooth, not extended ventrally; first and third supra-abdominal photophores about even and raised above second; first supra-anal markedly lower than second, which is lower than third; jaws medium; in preservative broad, dark, dorsal bar reaches to midline followed by light stripe which reaches mid-dorsal line; ventral border of dorsal pigment raised considerably above supra-anal photophores; dark pigment spots present on midline.

Distribution (Fig. 63). Known only from a specimen taken near the Seychelle Islands in the Indian Ocean; two juvenile *Polyipnus* from the east coast of Africa may represent this species. Note: Key characters checked with holotype through the courtesy of Dr. Verner Larsen, ZMUC.

DISCUSSION AND CONCLUSIONS

Patterns of Distribution

The ecological distinctness of the family and the basic structural modifications involved in the peculiar body form were discussed above. Given this basic structural similarity, the respective genera have diverged morphologically and ecologically. This is apparent in the distinctive distribution pattern of each genus and is indicative of the types of distributions to be found in deep-sea fishes.

Polyipnus. Although *Polyipnus* has the basic adaptive attributes of a midwater fish, the genus—with the exception of isolated expatriates—is associated with land areas. Land-oriented distributions have been reported in midwater fishes (Ebeling, 1962; Nafpaktitis, 1968), but these have involved members of essentially pelagic genera. *Polyipnus* is a moderately speciose genus which has adapted solely to land associated environments. While continental slope areas are important, this genus occurs abundantly near oceanic islands well away from continental margins. Depth data are generally sparse, but indicate that *Polyipnus* is found from 50 m to 400 m. The extent of diurnal migration is unknown, although certain species have been reported near the surface at night off Japan (Haneda, 1952). The "pseudopelagic" environment of this species has not been extensively sampled in most areas. Species ranges are therefore incomplete, and little is known about population structure and vertical distribution. New species can be expected and additional revision will be required as collecting proceeds.

The peculiar distribution of this genus may be related to land-oriented food chains. There is an extensive amount of literature on the increased productivity associated with land areas and on the

occurrence of neritic forms of zooplankton. *Polyipnus* has specialized feeding habits, and two peculiar morphological features may be involved in its adaptation to a specialized niche. These features are the jaw and branchial morphology, and the enlargement of the otic region. An additional indication of biological differences from the other genera is the small number of juveniles collected with the adults. Much remains to be known about the biology and ecology of this genus, as well as its "pseudopelagic" environment.

Comparison of the essentially tropical land-oriented distribution of *Polyipnus* with other tropical shore species provides some interesting parallels. Tropical reef and shelf fish are diverse in the Indo-west Pacific region, with the Indo-Malayan area the most speciose (e.g., Ekman, 1967: 17). The number of species declines as one proceeds from this area. While present in many of the islands of outer Polynesia (Hawaii, Marquesas, Tuamotu archipelago), few shore species reach the western coast of the Americas. This is attributed to the wide stretch of open water in the eastern Pacific (the zoogeographic east Pacific barrier). Contributions of Indo-west Pacific elements to the tropical Atlantic are reduced by a similar, although not as restrictive, central Atlantic barrier, in addition to the African continent (Briggs, 1960, 1961). The tropical shore fauna is further characterized by its "moderness." It consists primarily of the most advanced and latest evolved fishes, with relicts and more primitive groups less well represented. Geographic endemics are common, especially near the more isolated island groups.

The largest number of *Polyipnus* species have been collected around the Philippine Islands. Eight of 17 known species occur in the tropical west Pacific. Endemics occur in New Zealand, Hawaii, and the Marshall Islands at the limits of the range in the Pacific. Three other species occur in the western Indian Ocean, thus accounting for 14 of 17 species in the Indo-west Pacific. No species are reported from the eastern Pacific. The *P. spinosus* species complex is not found in the Atlantic; only three species occur there. Two are restricted to tropical and temperate America, and one to the west African coast. There are no trans-Panamanian species. Speciation tends to be geographic and endemics are numerous. Extensive sympatry between species complexes is rare. Life history features apparently restrict species to land-associated waters. No open-water pelagic populations are known, and barriers to gene flow among discontinuous populations appear considerable.

Here, then, is a classic tropical shore distribution in what appears to be the most primitive genus of the family (Ebeling, 1962, indicates some of the same features in *Melamphaes*). Since such a distribution is characteristic of lately evolved groups, it is interesting to speculate on the possible recent origin of *Polyipnus*. While primitive maurolicid gonostomatids are identified from the early Tertiary, *Polyipnus* as presently defined, is not. (It is not present in Tertiary Tethys or California deposits.) *Argyropelecus* is known from the Oligocene. Its distribution is worldwide (including the Tethys fauna), as are a number of gonostomatids (admittedly a different ecology and distribution pattern). *Polyipnus,* while primitive in axial skeleton characteristics, is nevertheless highly specialized in the cranial region. These characters may be the major adaptive features allowing *Polyipnus* access to its specialized niche, resulting in a new adaptive type which possibly arose relatively recently.

Argyropelecus. Argyropelecus species are characterized by broad worldwide high seas distributions. The genus is found in all tropical and temperate oceans, and is absent from polar seas. The limits of distribution are bounded approximately by the 5° isotherm at 200 m. Within these broad limits, however, distribution can be quite restricted with the result that worldwide species are broken up into a series of

disjunct populations which appear more or less isolated from each other.

In general, species occur vertically over the same depth range wherever they are found. With the exception of *A. gigas*, *Argyropelecus* species are partial or incomplete diurnal migrators. At night many species ascend to above 300 m, often to about 200 m from their daytime depths of 400–500 m. Catches in the upper 100 m seldom involve large numbers of individuals. *A. aculeatus* is most distinct in its vertical migration, while *A. gigas*, the deepest living species, migrates very little. Within these broad limits (150–600 m) depth variability is high, indicating considerable microcomplexity (Appendix B). From bathyscaphe observations during the day, Perès (1958) reports *A. hemigymnus* from 250–600 m, with large concentrations from 400–500 m. Perès' and other bathyscaphe observations (Drs. R. Rosenblatt, R. Haedrich, and R. Richards, personal conversations) indicate that *Argyropelecus* species do not school in the classical sense, but are somewhat isolated from one another. Catch data (Table 23) show the wide range in size distribution with large catches, another indication of nonschooling behavior.

Unlike many midwater fishes, the larvae and juveniles of *Argyropelecus* are found in the adult environment (Table 23) (Ahlstrom, 1959). Over the range of a species distribution some gravid females and young juveniles were usually found. Large scale expatriation does not appear to be important. Wherever a species is found in an area in numbers it seems to represent a breeding population.

Argyropelecus is represented by seven species in three species complexes. Species are morphologically distinct in most cases and, as with *Polyipnus*, broad sympatry within complexes is uncommon. Sympatry is limited to zones of mixing between allopatric species ranges when it occurs within species complexes. Dwarf and giant species occur. The giant species (*A. gigas*) is quite restricted in distribution, limited essentially to zones of water-mass boundaries. The dwarf species (*A. hemigymnus*), while occurring in the relatively unproductive central water masses, is abundant in highly productive temperate and eastern boundary current waters.

Sternoptyx. *Sternoptyx* species have broad worldwide pelagic distributions similar to *Argyropelecus* and with approximately the same geographic limits. The juveniles are found in the adult environment, although larger individuals may be found slightly deeper. There is no indication of expatriation. *Sternoptyx* is less speciose than *Argyropelecus* and species distinctions are much less marked. Two of the three species (*S. diaphana* and *S. obscura*) have wide allopatric ranges, with restricted areas of overlap. *S. pseudobscura* and *S. diaphana* are broadly sympatric over much of their respective ranges.

Vertically, all species are deep living (500–1500 m) and show little diurnal migration. Variability in catch size ranges indicates that *Sternoptyx* probably does not school.

Geographic Variation

Mayr (1963: 333) makes the following points in a discussion of geographic variation: Every population of a species differs from all other populations genetically, and when sufficiently sensitive tests are employed, also biometrically. The degree of divergence between different populations of a species ranges from near complete identity to distinctness almost of species level. Various characters of a species may and usually do differ independently. The characters of a given population have at least a partial genetic basis, and in most cases tend to remain rather constant through the years.

The absence of detectable differences between horizontally disjunct populations is not necessarily indicative of no population differences. In the present study, methods were not particularly sensitive, nor were many characters used. However,

where differences do exist one can delimit populations which, when coupled with distributional data, should add to our understanding of the environmental and biological factors which are important in restricting species distributions.

Most of the patterns of geographic variation outlined by Mayr are present in *Argyropelecus* and *Sternoptyx*. *A. gigas*, which appears to have the most disjunct distribution, displayed no detectable differences between widely separated populations. Characters which are constant in one species, vary in another. In general, however, population differences were found between geographically isolated populations as indicated by horizontal distributions. The statistical characteristics of a population of at least one species (*A. aculeatus*) remained constant over a period of two years. Population limits can be quite broad, and usually population boundaries are correlated with species boundaries in the same area. However, where species' ranges cross major zoogeographic boundaries, populations on either side of this boundary may be quite distinct (e.g., *A. hemigymnus* in the North Atlantic).

Population boundaries and morphological diversification are more obvious in the shallow-dwelling *Argyropelecus* than in the deeper-living and nonmigrating *Sternoptyx* (Ebeling and Weed, 1963, noted this for *Melamphaes* and *Scopelogadus*). Distributions of deeper living pelagic invertebrates also show this pattern (David, 1963; Grice and Hulsemann, 1967) which is apparently correlated with the decrease in environmental differences with depth between different areas of the oceans. Additional study is necessary to fully appreciate and delimit the population structure of both genera.

Distributional Factors

A considerable amount of literature is now available emphasizing the importance of water masses in the distribution of deep-sea organisms (Bieri, 1959; Ebeling, 1962; Johnson and Brinton, 1963, among others). Discussions of water masses—their formation, location, and identification—are numerous (e.g., Sverdrup et al., 1960; Ebeling, 1962), and each year knowledge of the extent, boundaries, and origin of discontinuities in the oceans increases. Table 24 relates the distribution of the species of *Argyropelecus* and *Sternoptyx* to the various water masses as presently defined. Several interesting conclusions result. One species (*A. aculeatus*) is limited to central water masses within the great gyre systems of the central oceans. Two species (*A. lychnus*, *S. obscura*) are limited to the east Pacific equatorial water mass and the transitional waters at its boundary. As presently defined, water masses are too broad to accurately describe many distributions; this is particularly so in the Atlantic. While the label "central" or "equatorial" is indicative of similarities between water masses in different areas, there can be significant differences in the faunal components (e.g., Indian equatorial versus east Pacific equatorial; east north Pacific central versus west north Pacific central).

Since the distributions of *Argyropelecus* and *Sternoptyx* are disjunct yet worldwide, a detailed look at the range of each species was made in an attempt to define some of the important distributional parameters. Temperature was considered, as it is often correlated with the distributional limits of fishes. Table 22 represents the temperature range of each species within arbitrarily selected depth limits, corresponding roughly to the depth limits of the species. Tables 20 and 21 illustrate temperature depth profiles from various parts of the ocean where different species occur. As Table 22 illustrates, absolute temperature ranges widely overlap, although certain species tend to be high while others are low. Species occur in colder waters in the Pacific in comparison with the Indian and Atlantic oceans. Dis-

TABLE 20. TEMPERATURE-DEPTH PROFILES FOR VARIOUS PARTS OF THE PACIFIC AND INDIAN OCEANS

Depth (m)	40°N, 150°W *Pacific subarctic*	34°N, 122°W *California*	10°N, 120°W *Eq Pacific*	18°N, 142°W *NE Pacific Cent*	25°N, 160°E *NW Pacific*
200	9.5	9	12	13	17
400	6.5	6.5	9.5	8	14
600	5	5	6	6.5	8
800	<5	<5	5.5	5	5
1000	<5	<5	4.5	<5	4.5

Depth (m)	30°S, 85°W *SE Pacific Chile*	25°S, 130°W *SE Pacific*	30°S, 160°E *SW Pacific*	40°S, 140°E *Subantarctic*	14°S, 115°E *Java*
200	11	17	21	8.5	14
400	7	11	12	7.5	9
600	6	6.5	9	7	
800	4.5	5.5	7	5	
1000	<5	5	4.5	4.5	

Depth (m)	4°N, 65°E *NC Indian*	35°S, 65°E *SC Indian*	35°S, 40°E *SW Indian*	12°S, 65°E *Eq Indian*	20°S, 100°E *SE Indian*
200	14	13	17	15	18
400	11	12	15	10	11
600	10	11	13	7.5	
800	8	9	10	6	
1000	7	6	7	5	
1200	5.5	<5	5	<5	

tributional generalities become more definite, however, upon examination of the horizontal distribution of the various species, coupled with the temperature profiles and general hydrographical characteristics.

The following pattern emerges by comparing the various species. *A. gigas* is limited to transitional waters at the boundaries of tropical central or warm water masses and colder temperate waters where roughly the 5° isotherm is deeper than 800 m. *A. affinis* and *A. sladeni* are

TABLE 21. TEMPERATURE-DEPTH PROFILES FOR VARIOUS PARTS OF THE ATLANTIC OCEAN.

Depth (m)	28°N, 87°W *N Gulf Mex*	24°N, 93°W *Gulf Mex*	17°N, 60°W *Venezuela*	16°N, 79°W *Caribbean*	32°N, 15°W *Trop NE Atl*	40°N, 20°W *N NE Atl*	40°N, 50°W *NW Atl*
200	14	20	15	18	16	13	16
400	9	10	9	11	13	12	12
600	6	8	7	7.5	11	10.5	8
800	5	7	5	6	10	9.5	6
1000	<5	6	<5	5	9	8	<5
1200	<5	5	<5	<5	8	7	<5

Depth (m)	*Gulf of Guinea*	8°N, 35°W *Trop Atl*	16°N, 25°W *Verdes Isl*	16°S, 60°W *SW Atl*	24°S, 70°W *SW Atl*	24°S, 5°E *SE Atl*
200	14	10	15	20	14	16
400	9	8	11	10	10	13
600	6	7	9	6	8	9
800	<5	6	7	<5	<5	5.5
1000	<5	5	6	<5	<5	<5
1200	<5	<5	5.5	<5	<5	<5

TABLE 22. TEMPERATURE RANGES AT ARBITRARILY CHOSEN DEPTHS FOR THE VARIOUS SPECIES OF *ARGYROPELECUS* AND *STERNOPTYX*. FIGURES WERE OBTAINED BY COMPARING HORIZONTAL SPECIES RANGES WITH KNOWN TEMPERATURE-DEPTH PROFILES OVER THIS RANGE.

Species	Depth (m)	Temperature Range (°C)
A. aculeatus	200	15–21 (all oceans)
	400	10–15 (all oceans)
A. olfersi	200	12–13 (all oceans)
	400	9 (Atlantic) 7 (Pacific)
A. lychnus	200	7–12 (Pacific)
	400	6–10 (Pacific)
A. sladeni	200	9–14 (all oceans)
	400	6.5–11 (all oceans)
A. hemigymnus	200	9–18 (all oceans)
	400	6.5–13 (all oceans)
A. affinis	200	9–14 (all oceans)
	400	6.5–11 (all oceans)
A. gigas	400	7–12 (all oceans)
	600	6–10 (all oceans)
S. diaphana	600	5–7 (Pacific); 9–11 (Indian & Atlantic)
	800	5–4.5 (Pacific); 7.5–10 (Indian & Atlantic)
S. obscura	600	7.5–10 (Indian & Pacific)
	800	6–8 (Indian); 4.5–5.5 (Pacific)
	1000	4.5–5 (Indian & Pacific)
S. pseudobscura	800	8–5 (all oceans)
	1000	4–5 (all oceans)

restricted primarily to the eastern boundary currents and areas of upwelling which are characterized by cool water between 300 m and 400 m. *A. olfersi* is restricted to the warmer areas of subpolar waters characterized by 12–13° temperatures at 200 m. *A. hemigymnus* is excluded only from equatorial waters, although biometric data indicates a population structure which corresponds to water mass boundaries. *A. aculeatus* is restricted to warm central water masses in areas bounded approximately by the 15° isotherm at 200 m. *A. lychnus* occurs only in the Pacific equatorial water mass characterized by cool temperatures between 200 m and 400 m. *S. diaphana* is excluded from the equatorial water masses only. *S. obscura* is limited to equatorial water masses and their boundaries while *S. pseudobscura* is similar to *S. diaphana*, although more restricted to tropical and subtropical waters.

The above distribution pattern is a strong argument for the importance of

TABLE 23. CATCH STATISTICS FOR TWO LARGE SAMPLES OF *ARGYROPELECUS* FROM THE NORTH ATLANTIC. SIZE CLASS FIGURES REFER TO THE NUMBER OF INDIVIDUALS IN THE SAMPLE WHOSE STANDARD LENGTH FALLS BETWEEN THE SIZE LIMITS; I.E., THERE WERE TWO INDIVIDUALS OF *A. ACULEATUS* WHOSE STANDARD LENGTHS WERE FROM 21 TO 25 MM.

		Size Class (mm)									
Species	Total Catch	10	15	20	25	35	45	55	65	90	90+
*A. hemigymnus**	240	9	61	37	43	80	10				
*A. aculeatus***	75			3	2	6	13	29	15	8	1

* Atlantis II 13, station 1040, 0940–1125, 320–375 m.
** Chain 32, station 859, 0835–1305, 380 m.

TABLE 24. OCCURRENCE OF THE SPECIES OF *ARGYROPELECUS* AND *STERNOPTYX* IN VARIOUS WATER MASSES. X = TAKEN IN NUMBERS; S = REPORTED IN SMALL NUMBERS USUALLY NEAR WATER MASS BOUNDARIES; O = UNRECORDED; ? = POSSIBLE RECORD.

	Species									
Water Mass	*A. gigas*	*A. affinis*	*A. hemigymnus*	*A. lychnus*	*A. sladeni*	*A. aculeatus*	*A. olfersi*	*S. diaphana*	*S. obscura*	*S. pseudobscura*
N Atlantic Central	X	X	X	O	X	X	X	X	O	X
S Atlantic Central	X	X	X	O	X	X	S	X	O	X
EN Pacific Central	O	X	X	O	X	O	O	X	O	X
WN Pacific Central	O	O	S	O	O	S	O	X	O	O
ES Pacific Central	S	O	S	O	O	X	S	X	O	X
WS Pacific Central	O	O	S	O	X	X	O	O	O	O
NE Pacific Transitional	O	X	X	X	X	O	O	S	X	O
SE Pacific Transitional	X	X	X	X	X	S	S	X	X	O
Pacific Equatorial	O	S	O	X	O	O	O	S	X	O
Indian Equatorial	S	X	X	O	X	O	O	O	X	S
Indian Central	X	S	X	?	S	X	O	X	S	X
Subantartic	X	O	X	O	O	O	X	X	O	O
N Pacific Subarctic	O	O	X	O	X	O	O	X	O	O

temperature in defining distributions (e.g., McGowan, 1960; Nafpaktitis, 1968). It is apparent, however, that absolute temperature values per se are not the sole limiting factor and that each water mass can be defined by a host of other physical and biological factors, all of which may be important in limiting distributions.

A number of recent studies indicate that water masses have a biological identity and many widely diverse forms are limited to them (Bieri, 1959; Aron, 1962; Brinton, 1962; McGowan, 1963; Fager and McGowan, 1963). Additional aspects to be considered are the hydrographic features such as boundary areas, transitional waters and upwelling areas which provide further heterogeneity of biological importance. Pelagic hatchetfish distributions are particularly illustrative of the biological similarities of areas with corresponding hydrographic properties. For instance, eastern boundary currents which are quite similar hydrographically (Wooster and Reid, 1963) contain the same hatchetfish species wherever they are found. The same can be said of central gyre areas or subpolar waters.

While the physical and biological proper- ties of the whole water column are im- portant in the ecology of a given wate mass, barriers to distribution in hatchet fishes appear to be primarily a function o the environmental properties over th depth range of the species. Furthermore the barriers become less marked witl depth so that discontinuities at 800–100 m occur less often than those from 200- 400 m. This is reflected in the broa distributions of the deep living *Sternoptyx* with three closely related species com pared to the highly disjunct and mor speciose *Argyropelecus* with its more shal low distribution. This same pattern is evi dent in other deep living forms (David 1963; Ebeling, 1962; Grice, 1963; Grice an Hulsemann, 1967) where life histor features of juveniles or larvae do not com plicate the distribution.

Zoogeographic Regions

Several features make the pelagic hatchet fishes particularly well suited to zoogeo graphical studies. Their distributions ar broad, yet limited to waters of simila

TABLE 25. ZOOGEOGRAPHIC REGIONS.

No.	Region	Species Assembly
1.	E Pacific Equatorial	*A. lychnus, S. obscura.*
2.	N Pacific Transitional	*A. affinis, A. hemigymnus, A. sladeni, S. obscura, A. lychnus (S. diaphana).*
3.	Pacific Subarctic	*A. sladeni, A. hemigymnus (S. diaphana).*
4.	EN Pacific Central	*A. affinis, A. sladeni, A. hemigymnus, S. diaphana.*
5.	WN Pacific Central	*A. aculeatus, A. hemigymnus, S. diaphana, S. pseudobscura.*
6.	SE Pacific Transitional	*A. affinis, A. sladeni, A. hemigymnus, A. lychnus, A. gigas, S. diaphana (A. olfersi, S. obscura).*
7.	Pacific Subantarctic	*A. olfersi, A. hemigymnus, A. gigas, S. diaphana.*
8.	S Pacific Central	*A. aculeatus, A. hemigymnus (S. pseudobscura).*
9.	Indian Equatorial	*A. affinis, A. sladeni, A. hemigymnus, S. obscura.*
0.	Java-Indonesian	*A. affinis, A. sladeni, A. hemigymnus, S. diaphana, S. obscura.*
1.	Indian Central	*A. aculeatus, A. hemigymnus, A. gigas, S. diaphana, S. pseudobscura.*
2.	Tropical Atlantic	*A. sladeni, S. diaphana, S. pseudobscura (A. hemigymnus).*
3.	SE Atlantic Transitional	*A. affinis, A. sladeni, A. gigas, A. diaphana, S. pseudobscura.*
4.	Venezuelan-Caribbean	*A. affinis, A. sladeni, A. hemigymnus, S. diaphana, S. pseudobscura, A. aculeatus.*
5.	Caribbean-Gulf Central	*A. aculeatus, A. hemigymnus, S. diaphana, S. pseudobscura, A. sladeni.*
6.	Gulf Peripheral	*A. affinis, A. sladeni, A. hemigymnus, A. gigas, S. diaphana.*
7.	NW Atlantic Pocket	*A. affinis, A. sladeni, S. diaphana, S. pseudobscura.*
8.	WN Atlantic Central	*A. aculeatus, A. hemigymnus, S. diaphana (A. gigas).*
9.	EN Atlantic Central	*A. aculeatus, A. hemigymnus, S. diaphana, S. pseudobscura (A. gigas).*
:0.	NE Atlantic Subarctic	*A. olfersi, A. hemigymnus, A. gigas, S. diaphana, S. pseudobscura.*
:1.	SW Atlantic Central	*A. aculeatus, A. hemigymnus, S. diaphana, S. pseudobscura (A. sladeni).*
:2.	W Mediterranean	*A. hemigymnus.*
:3.	N New Zealand Pocket	*A. sladeni.*
:4.	SE Atlantic Subantarctic	*A. olfersi, A. hemigymnus, S. diaphana.*

ıydrographic properties; they are relatively ıumerous and easily caught; expatriation is imited; adults and juveniles share the same ·nvironment; they are only partial migrators ıt best and are thus less affected by seasonal luctuations; and they occur over much of he depth range of the "mesopelagic" envi-onment.

As we have seen above, the water masses as presently defined are too broad to explain species distributions as we find them. However, the concept of water masses as bodies of water with similar hydrographic and biological properties is important, and seems to be the most significant one in explaining much of the heterogeneity in the midwater environment. The pelagic hatchetfishes are used in Figure 80 as

indicator species of waters of similar properties and their associated discontinuities. The results may add to greater appreciation of water masses—both conceptually and geographically. Table 25 and Figure 80 list the zoogeographic regions and are also an attempt to indicate similarities between regions. The characteristic species assemblages which occur in these regions are listed under the appropriate area. No boundaries were drawn because in most cases they could not be defined. Important isotherms are included and may serve as rough boundaries. Presently defined water mass boundaries (see Sverdrup et al., 1960) in many cases mark the limits of these areas.

Several attempts at defining oceanic zoogeographic regions have been made (Ebeling, 1962; Clarke, 1966) and Figure 80 represents an additional one. No attempt has been made to categorize these regions as primary or secondary, but certainly some regions involve the whole of the mesopelagic environment, while others seem important only at shallower depths. Considerable variation exists in the sharpness of the boundaries and, to some extent, in the degree of species overlap. As knowledge of the oceans and their fauna increases, the nature and extent of these regions and their boundaries will become more apparent.

Areas which are zoogeographic regions and have boundaries which appear throughout the "mesopelagic" environment are the tropical east Pacific, the Indian equatorial region, the northeast Atlantic, and the subantarctic, especially the Pacific portion. There is a wide subtropical belt that is continuous at deeper depths, but is broken into smaller regions above approximately 600 m. The tropical east Pacific has been recognized as a major zoogeographic region, and it seems to have an endemic fauna at all levels (Brinton, 1962; Ebeling, 1962; Johnson and Brinton, 1963). The Indian equatorial region, while not as well known, appears to be somewhat similar to the equatorial Pacific, at least in some species of hatchetfishes and other fishes as well (Ebeling, 1962; Gibbs and Hurwitz, 1967). The northeast Atlantic is quite different from the western Atlantic in a number of groups (Haffner, 1952; Clarke, 1966; Nafpaktitis, 1968). Additional evidence from this and other studies (Alvarino, 1965; Gibbs, 1968) indicates that the convergence area, especially in the South Pacific, is a major zoogeographical region which may be quite restricted in the South Atlantic and Indian Ocean. The 5° isotherm is much closer to the central water masses at 200 m (Fig. 80), and the distance between the convergences is generally less broad (Sverdrup, 1960).

Regions which are distinctive for the upper 500 m are the warm central water masses of the major gyre systems, and the eastern boundary currents which are cold water areas of transition and upwelling. There are other smaller areas that are important zoogeographically and are faunally similar to the major regions. These include pockets of cold water around the Gulf of Mexico, off South Africa, off the southeast United States (see Haffner on *Chauliodus*, 1952), in the southern Caribbean and tropical Atlantic, off Java, off New Zealand, and southeast of Hawaii.

The Sternoptychidae are represented by a single species in the western Mediterranean, an area which seems distinct from the warmer eastern end. This population is distinct from the North Atlantic one, and this distinction has been documented for other midwater fishes (Marshall, 1963). Hatchetfishes have not been taken in the Red Sea proper (Marshall, 1963) or the Gulf of California (Lavenberg and Fitch, 1966).

Ecological niches and diversity. Speciation pattern, distribution, and population structure are three indicators of diversity, niche breadth, and heterogeneity in the mesopelagic environment. While the worldwide midwater environment is heterogene-

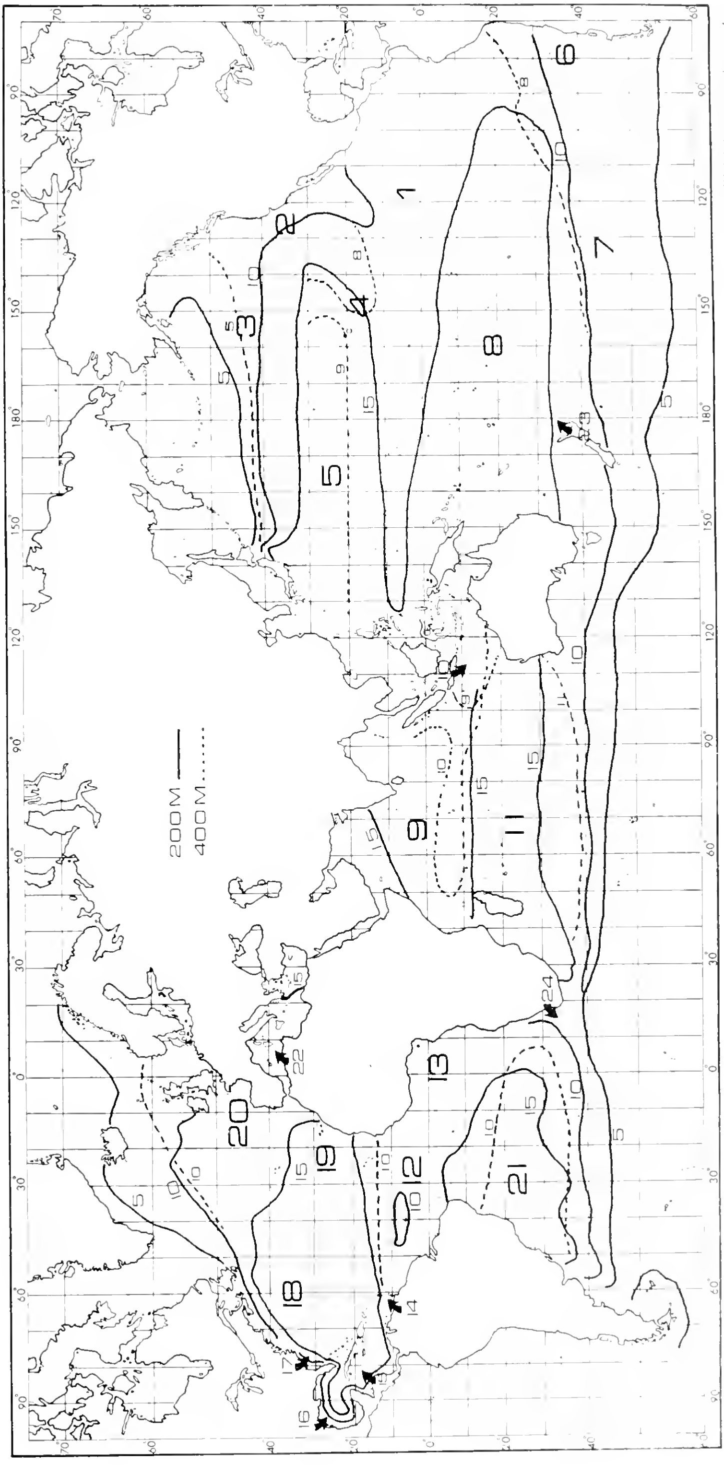


Figure 80. Zoogeographic regions of the mid-depths of the oceans determined from distributions of pelagic hatchetfishes. Solid lines mark isotherms at 200 m; broken lines mark 400 m isotherms. See text and Table 25 for explanation.

ous, it nevertheless appears to be relatively constant, at least in measurable physical parameters, over broad areas. This is reflected in the patterns observed in the three indicators mentioned above.

Measurable niche parameters appear quite broad in hatchetfishes in comparison with freshwater or shore faunas. Overlap between congeneric species is not extensive, and where it does occur there are usually major morphological or vertical distributional differences. Allopatric ranges are the rule. Congeneric coexistence usually requires either a major shift in depth distribution or marked morphological change. Thus *Polyipnus*—often geographically isolated and land associated—is the most speciose genus, while *Sternoptyx*—the deepest living—is the least. There are indications that this broad niche phenomenon occurs in other groups as well (Marshall, 1963).

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SUMMARY

1. The Sternoptychidae are primitive stomiatoid fishes closely related to the Gonostomatidae, but different from them morphologically; most of this difference is related to the peculiar deep body shape of the former.
2. The Sternoptychidae probably arose during the early Tertiary as part of an early stomiatoid radiation. Miocene fossils of *Argyropelecus* could not be distinguished from their modern counterparts, indicating little osteological evolution in this genus since then.
3. The three genera in the family are widely divergent; each has specialized in a separate direction.
4. *Polyipnus* occurs only in close association with land. Its pattern of distribution and speciation closely parallels that of many tropical shore species.
5. *Argyropelecus* is distributed widely in all tropical and temperate seas. It is a partial migrator not often entering the upper 100 m at night. Adults and juveniles are found in about the same depth range. *Argyropelecus* inhabits the upper "mesopelagic" zone (100–600 m).
6. *Sternoptyx* is distributed horizontally within the same limits as *Argyropelecus*. It inhabits the lower "mesopelagic" zone (500–1500 m) and does not appear to migrate diurnally.
7. *Argyropelecus* and *Sternoptyx* species are restricted in distribution, each species seemingly restricted to waters with similar hydrographic and biological properties.
8. *Argyropelecus* is more speciose and shows more morphological variation than *Sternoptyx*. Species ranges in *Sternoptyx* are much broader, indicating that barriers to distribution and heterogeneity may be more pronounced in the upper "mesopelagic" than in the lower.
9. Certain species assemblages occur in waters which are hydrographically similar. These assemblages are used to zoogeographically define distinct areas of the world's oceans.
10. Ecological niches in the Sternoptychidae are broad over measurable niche parameters. Allopatric species ranges are the rule and, where congeneric sympatric species occur, there is usually a considerable amount of morphological or vertical distinctness.

APPENDIX A

INSTITUTIONS AND CRUISES FROM WHICH MATERIAL WAS EXAMINED OR RECORDED

I. Institutions and their abbreviations.

Collections of T. Abe and O. Suzuki, Tokyo, Japan.	ABE
Australian Museum, Sidney, Australia.	AM
Bureau of Commercial Fisheries, Honolulu, Hawaii.	BCFH
Bureau of Commercial Fisheries, La Jolla, California.	BCFL
Bureau of Commercial Fisheries, Miami, Florida.	BCFM
British Museum (Natural History), London, England.	BMNH
Dominion Museum, Wellington, New Zealand.	DMNZ
International Indian Ocean Expedition.	IIOE
Biologische Anstalt Helgoland (Meteor Indian Ocean Expedition), Hamburg, Germany.	IOES
Los Angeles County Museum, Los Angeles, California.	LACM
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.	MCZ

Appendix A (Continued)

Musée National d'Histoire Naturelle, Paris, France.	MNHNP
Musée Royale d'Afrique Central, Tervuren.	MRAC
National Institute of Oceanography, Surrey, England.	NIO
Oceanographic Data Center, Washington, D.C.	ODC
Scripps Institute of Oceanography, La Jolla, California.	SIO
Institute of Marine Science, University of Miami, Florida.	UMML
John Hancock Foundation, University of Southern California, Los Angeles, California.	USC
U.S. National Museum, Washington, D.C.	USNM
Woods Hole Oceanographic Institute, Woods Hole, Massachusetts.	WHOI
Zoological Museum, Copenhagen, Denmark.	ZMUC

2. Institutions and Cruises from Which Material Was Examined and Recorded.

Institution	Ship and Cruise	Location
ABE	local fishing vessels	Japan
AM	holotypes only	Australia
BCFH	HUGH M. SMITH 30	C Pacific
	HUGH M. SMITH 31	C Pacific
BCFL	larval and juveniles only	EN Pacific
BCFM	GERONIMO	Tropical Atlantic
	SILVER BAY	Florida, Gulf of Mexico
	OREGON	Gulf of Mexico
BMNH	DISCOVERY and others	Worldwide
DMNZ	TUI	New Zealand
HOE	ANTON BRUUN 3 and 6	Indian Ocean
IOES	METEOR (holotype description)	Indian Ocean
LACM	VELERO	NE Pacific
MCZ	ATLANTIS, CAPTAIN BILL III	N Atlantic
	GOSNOLD, BRUUN 13,	Chile, Tropical Atlantic
	CHAIN 17–49, miscellaneous collections	Mediterranean
MNHNP	holotypes only	Atlantic
MRAC	holotype	W African Coast
NIO	DISCOVERY (1955–1965)	NE Atlantic, Indian Ocean
ODC	USNS GILLISS	N Atlantic, Caribbean
SIO	COBB 208, 303	NE Pacific
	BLACK DOUGLASS 203, 303	NE Pacific
	HORIZON	N Pacific
	HOLIDAY, TETHYS	C & S Pacific
	MONSOON, BAIRD	C & S Pacific
UMML	GERDA	Florida, Gulf of Mexico
	PILLSBURY	Caribbean, Gulf of Guinea
USC	USNS ELTANNIN	Subantarctic, Pacific
USNM	ALBATROSS, OREGON	Atlantic, Pacific
	SILVER BAY, COMBAT	
WHOI	CHAIN 60, 72, ATLANTIS II 13	Caribbean, Gulf of Mexico
	ATLANTIS II 31	N & SW Atlantic
ZMUC	GALATHEA	World Cruise
	THOR and miscellaneous collections	N Atlantic, Mediterranean

APPENDIX B

EPTH TABLES OF THE SPECIES OF *ARGYROPELECUS* AND *STERNOPTYX*. DEPTH DATA FOR THESE TABLES EPRESENT MAXIMUM NET DEPTHS ONLY. "CATCH" REFERS TO THE NUMBER OF HAULS IN WHICH THE UMBER OF FISH TAKEN IS SHOWN HORIZONTALLY BETWEEN THE FIGURE LISTED AND THE PREVIOUS FIGURE. DEPTH" REFERS TO THE MAXIMUM NET DEPTHS AND IS RECORDED VERTICALLY BETWEEN THE DEPTH LISTED ND THE ONE LISTED ABOVE IT. "ZERO" CATCH REFERS TO THE NUMBER OF NEGATIVE TOWS FOR THAT SPECIES. "+" MEANS GREATER THAN OR EQUAL TO THE VALUE LISTED.

Argyropelecus affinis

Night

epth	Catch 0	5	10	20	50	100	100+	N
100	36	1	0	0	0	0	0	1
200	5	1	0	1	1	0	0	3
300	13	7	1	1	0	0	0	9
400	0	0	0	0	0	0	0	0
500	4	2	0	0	0	0	1	3
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
000	0	0	0	0	0	0	0	0
000	0	3	0	1	0	0	0	4
001+	0	0	0	0	0	0	0	0

alifornia, Chile (Pacific)

Depth	Catch 0	5	10	20	50	100	100+	N
100	20	1	0	0	0	0	0	1
200	10	0	0	0	0	0	0	0
300	9	1	0	0	0	0	0	1
400	1	1	0	0	1	0	0	2
500	2	2	0	1	0	0	0	3
600	0	0	0	0	0	0	0	0
700	1	2	0	0	0	0	0	2
1000	3	0	0	0	0	0	0	0
2000	0	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Gulf of Guinea, Caribbean

Day

epth	Catch 0	5	10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	5	0	0	0	0	0	0	0
400	19	1	1	0	0	0	0	2
500	7	2	1	1	0	0	0	4
600	1	2	0	1	0	0	0	3
700	2	1	0	0	0	0	0	1
000	5	1	0	0	0	0	0	1
000	6	4	0	0	0	0	0	4
001+	1	0	0	0	0	0	0	0

ulf of Mexico, Gulf of Guinea, Caribbean

Depth	Catch 0	5	10	20	50	100	100+	N
100	9	0	0	0	0	0	0	0
200	10	0	0	0	0	0	0	0
300	14	3	0	0	0	0	0	3
400	7	0	0	0	0	1	0	1
500	5	0	0	1	2	0	0	3
600	4	0	0	0	0	0	0	0
700	0	3	0	0	0	0	0	3
1000	10	0	0	0	0	0	0	0
2000	19	3	0	0	0	0	0	3
2001+	7	0	0	0	0	0	0	0

California, Chile (Pacific)

Argyropelecus gigas

Night

epth	Catch 0	5	10	20	50	100	100+	N
100	30	0	0	0	0	0	0	0
200	26	0	0	0	0	0	0	0
300	19	0	0	0	0	0	0	0
400	9	0	0	0	0	0	0	0
500	21	1	0	0	0	0	0	1
600	7	0	1	0	0	1	0	2
700	4	1	0	0	0	0	0	1
000	14	0	0	0	0	0	0	0
000	4	1	0	0	0	0	0	1
001+	0	0	0	0	0	0	0	0

tlantic

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	3	0	0	0	0	0	0	0
200	7	0	0	0	0	0	0	0
300	10	0	0	0	0	0	0	0
400	34	0	1	0	0	0	0	1
500	25	0	1	0	0	0	0	1
600	12	2	0	0	0	0	0	2
700	8	1	0	0	0	0	0	1
1000	20	2	0	0	0	0	0	2
2000	5	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Atlantic

Appendix B (Continued)

Argyropelecus hemigymnus (Form A)

Night

Depth	Catch 0	5	10	20	50	100	100+	N
100	20	1	0	0	0	0	0	1
200	9	1	0	0	0	0	0	1
300	11	0	0	0	0	0	0	0
400	2	0	0	0	0	0	0	0
500	4	0	0	0	1	0	0	1
600	0	0	0	0	0	0	0	0
700	3	0	0	0	0	0	0	0
1000	3	0	0	0	0	0	0	0
2000	2	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Caribbean and Gulf of Mexico

Depth	Catch 0	5	10	20	50	100	100+	N
100	23	7	1	1	0	0	0	9
200	29	0	0	2	0	0	0	2
300	20	0	0	0	0	2	0	2
400	8	1	1	0	2	0	0	4
500	23	0	1	1	0	0	0	2
600	14	0	0	0	0	0	0	0
700	5	3	1	0	0	0	0	4
1000	22	1	0	0	0	0	0	1
2000	5	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

North Atlantic (see Day)

Depth	Catch 0	5	10	20	50	100	100+	N
100	5	0	0	0	0	0	0	0
200	3	0	0	0	0	0	0	0
300	4	1	0	0	0	0	0	1
400	16	2	1	1	1	0	0	5
500	3	0	0	1	0	0	0	1
600	2	0	0	0	0	0	0	0
700	5	2	0	0	0	0	0	2
1000	8	2	1	0	0	0	0	3
2000	11	2	2	0	0	0	0	4
2001+	6	1	1	0	0	0	0	2

Southern Ocean (Pacific)

Depth	Catch 0	5	10	20	50	100	100+	N
100	35	2	0	0	0	0	0	2
200	7	0	0	0	0	0	0	0
300	7	7	2	0	1	0	0	10
400	0	0	0	0	0	0	0	0
500	7	0	0	0	0	0	0	0
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	0	0	0	0	0	0	0	0
2000	3	1	0	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

Pacific (California)

Argyropelecus hemigymnus (Form A)

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	2	0	1	0	0	0	0	1
200	8	0	0	0	0	1	0	1
300	10	0	0	1	1	0	0	2
400	12	3	1	2	2	0	2	10
500	15	7	3	4	3	3	1	21
600	10	2	1	3	2	1	0	9
700	4	0	0	0	2	1	0	3
1000	25	3	0	1	0	0	0	3
2000	6	0	1	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

North Atlantic (20–40 N, 5–70 W)

Depth	Catch 0	5	10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	2	1	0	2	0	0	0	3
400	11	3	3	3	0	0	0	9
500	4	3	1	1	1	0	0	6
600	2	1	0	0	1	0	0	1
700	3	1	0	0	0	0	0	1
1000	6	1	0	0	0	0	0	0
2000	10	0	0	0	0	0	0	0
2001+	1	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	1	0	0	0	0	0	1
200	1	1	0	0	0	0	0	1
300	3	1	0	0	0	0	0	1
400	0	3	0	0	0	0	0	3
500	0	2	0	0	0	0	0	2
600	1	1	0	0	0	1	0	2
700	0	1	0	0	0	0	0	1
1000	2	1	2	1	1	0	0	8
2000	4	6	1	0	1	0	0	8
2001+	3	3	0	0	0	0	0	3

Southern Ocean (Pacific)

Depth	Catch 0	5	10	20	50	100	100+	N
100	8	0	0	0	0	0	0	0
200	8	0	0	0	0	0	0	0
300	11	1	0	1	0	0	0	2
400	4	0	1	0	0	0	0	1
500	3	2	1	0	0	0	0	3
600	1	0	0	0	0	0	0	0
700	1	2	0	0	0	0	0	2
1000	0	0	0	0	0	0	0	0
2000	3	7	0	0	0	0	0	7
2001+	0	1	0	0	0	0	0	1

Pacific (California)

APPENDIX B (Continued)

Argyropelecus hemigymnus (Form B)

Night

Depth	0	5	Catch 10	20	50	100	100+	N
100	21	0	0	0	0	0	0	0
200	10	0	0	0	0	0	0	0
300	9	2	0	0	0	0	0	2
400	2	0	0	0	0	0	0	0
500	3	2	0	0	0	0	0	2
600	0	0	0	0	0	0	0	0
700	3	0	0	0	0	0	0	0
1000	3	0	0	0	0	0	0	0
2000	2	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Depth	0	5	Catch 10	20	50	100	100+	N
100	27	3	1	0	1	0	0	5
200	21	6	2	2	0	0	0	4
300	17	1	0	0	2	0	0	2
400	7	1	2	0	0	1	0	4
500	2	1	1	1	0	0	0	3
600	0	2	4	0	1	0	0	5
700	4	0	1	0	0	0	0	1
1000	14	2	0	3	1	0	0	6
2000	1	0	1	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

North Atlantic (see Day)

Depth	0	5	Catch 10	20	50	100	100+	N
100	5	0	0	0	0	0	0	0
200	2	1	0	0	0	0	0	1
300	3	2	0	0	0	0	0	2
400	8	8	1	2	1	1	0	13
500	0	1	0	1	0	2	0	4
600	1	0	0	1	0	0	0	1
700	4	1	2	0	0	0	0	3
1000	3	4	2	1	1	0	0	8
2000	5	9	1	0	0	0	0	10
2001+	5	0	2	1	0	0	0	3

Southern Ocean (Pacific)

Argyropelecus hemigymnus (Form B)

Day

Depth	0	5	Catch 10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0
200	10	0	0	0	0	0	0	0
300	14	0	0	0	0	0	0	0
400	22	0	0	0	0	0	1	1
500	31	1	1	0	0	0	0	1
600	14	3	3	0	0	0	0	6
700	11	0	0	1	0	0	0	1
1000	29	1	0	0	0	0	0	1
2000	7	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

N Atlantic (20°–40°N, 5°–70°W)

Depth	0	5	Catch 10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	2	0	0	0	0	0	0	0
300	3	1	0	0	0	0	0	1
400	3	0	0	0	0	0	0	0
500	2	0	0	0	0	0	0	0
600	2	0	0	0	0	1	0	1
700	1	0	0	0	0	0	0	0
1000	9	1	0	0	0	0	0	1
2000	10	2	0	0	0	0	0	2
2001+	6	0	0	0	0	0	0	0

Southern Ocean (Pacific)

Depth	0	5	Catch 10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	5	0	0	0	0	0	0	0
400	20	0	0	0	0	0	0	0
500	10	0	0	0	0	0	0	0
600	3	1	0	0	0	0	0	1
700	4	0	0	0	0	0	0	0
1000	7	0	0	0	0	0	0	0
2000	10	0	0	0	0	0	0	0
2001+	1	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Appendix B (Continued)

Argyropelecus aculeatus

Night

North Atlantic

Depth	0	5	Catch 10	20	50	100	100+	N
100	25	4	2	1	0	0	0	7
200	18	10	2	0	1	0	0	13
300	21	0	1	0	0	0	0	1
400	8	3	1	0	0	0	0	4
500	17	7	1	0	0	0	0	8
600	8	6	0	0	0	0	0	6
700	0	7	2	0	0	0	0	9
1000	20	3	0	0	0	0	0	3
2000	5	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Depth	0	5	Catch 10	20	50	100	100+	N
100	8	6	1	0	2	0	0	9
200	0	3	3	1	1	2	0	10
300	5	3	0	2	0	0	0	5
400	0	0	0	0	0	0	0	0
500	2	1	0	0	0	0	0	1
600	0	0	0	0	0	0	0	0
700	2	0	0	0	0	0	0	0
1000	2	1	0	0	0	0	0	1
2000	0	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Day

North Atlantic (20°–40°N; 5°–70°W)

Depth	0	5	Catch 10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0
200	7	2	1	0	0	0	0	3
300	9	5	0	0	0	0	0	5
400	6	8	4	0	4	1	0	17
500	10	17	1	4	2	0	0	24
600	10	8	0	0	2	0	0	10
700	9	4	0	0	0	0	0	4
1000	24	6	0	1	0	0	0	7
2000	6	0	0	1	0	0	0	1
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Depth	0	5	Catch 10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	0	3	1	0	0	0	0	4
400	4	3	2	0	7	0	0	12
500	3	3	0	1	2	0	0	6
600	1	1	0	0	0	0	0	1
700	1	0	0	0	0	0	0	0
1000	2	1	0	0	0	0	0	1
2000	4	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Argyropelecus olfersi

Night — Atlantic and Southern Ocean

Depth	0	5	Catch 10	20	50	100	100+	N
100	34	1	0	0	0	0	0	1
200	23	4	2	0	0	0	0	6
300	21	2	1	0	0	0	0	3
400	22	6	0	0	0	0	0	6
500	21	2	1	0	0	0	0	1
600	7	2	0	0	0	0	0	2
700	1	0	0	0	0	0	0	0
1000	24	1	0	0	0	0	0	1
2000	17	1	0	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

Day — Atlantic and Southern Ocean

Depth	0	5	Catch 10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0
200	8	0	1	0	0	0	0	1
300	13	1	0	0	0	0	0	1
400	20	2	0	0	0	0	0	2
500	26	1	0	0	0	0	0	1
600	13	0	1	0	0	0	0	1
700	9	0	0	0	0	0	0	0
1000	26	3	0	0	0	0	0	3
2000	13	4	0	0	0	0	0	4
2001+	0	0	0	0	0	0	0	0

Argyropelecus sladeni

Night

Gulf of Mexico, Caribbean, Gulf of Guinea

Depth	0	5	Catch 10	20	50	100	100+	N
100	19	1	0	1	0	0	0	2
200	10	0	0	0	0	0	0	0
300	3	5	1	1	0	0	0	7
400	0	1	0	0	0	0	0	1
500	3	2	0	0	0	0	0	2
600	0	0	0	0	0	0	0	0
700	2	1	0	0	0	0	0	1
1000	3	0	0	0	0	0	0	1
2000	0	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Pacific (California)

Depth	0	5	Catch 10	20	50	100	100+	N
100	35	3	0	0	0	0	0	3
200	6	1	2	0	0	0	0	3
300	7	10	2	0	0	0	0	12
400	13	6	1	0	1	0	0	8
500	7	4	0	0	0	0	0	4
600	2	0	0	0	0	0	0	0.
700	7	0	0	0	0	0	0	0
1000	11	0	0	0	0	0	0	0
2000	2	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Appendix B (Continued)

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	4	2	0	0	0	0	0	2
400	8	6	3	2	1	0	0	12
500	6	3	1	0	0	0	0	4
600	7	1	1	0	0	0	0	2
700	1	3	0	0	0	0	0	3
1000	3	4	0	0	0	0	0	4
2000	7	3	0	0	0	0	0	3
2001+	0	1	0	0	0	0	0	1

Gulf of Mexico, Caribbean, Gulf of Guinea

Depth	Catch 0	5	10	20	50	100	100+	N
100	8	0	0	0	0	0	0	0
200	7	1	0	0	0	0	0	1
300	6	8	0	0	0	0	0	8
400	4	0	0	1	0	0	0	1
500	3	3	0	1	0	0	0	4
600	1	0	0	0	0	0	0	0
700	1	2	0	0	0	0	0	2
1000	0	0	0	0	0	0	0	0
2000	8	2	0	0	0	0	0	2
2001+	1	0	0	0	0	0	0	0

Pacific (California)

Argyropelecus lychnus

Night

Depth	Catch 0	5	10	20	50	100	100+	N
100	42	2	0	0	0	0	0	2
200	10	3	0	1	0	0	0	4
300	17	4	2	1	0	0	0	7
400	23	9	0	4	0	0	0	13
500	7	2	2	0	0	0	0	4
600	2	0	0	0	0	0	0	0
700	7	0	0	0	0	0	0	0
1000	11	0	0	0	0	0	0	0
2000	18	1	0	0	0	0	0	1
2001+	8	0	0	0	0	0	0	0

California, Chile, Tropical Pacific

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	10	0	0	0	0	0	0	0
200	10	0	0	0	0	0	0	0
300	13	3	1	0	1	0	0	5
400	9	0	0	0	0	0	0	0
500	6	2	0	0	0	0	0	2
600	4	0	0	0	0	0	0	0
700	2	2	0	0	0	0	0	2
1000	10	0	0	0	0	0	0	0
2000	21	1	0	0	0	0	0	1
2001+	7	0	0	0	0	0	0	0

California, Chile, Tropical Pacific

Sternoptyx obscura

Night

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	8	2	0	0	0	0	0	2
300	0	0	0	0	0	0	0	0
400	4	1	0	0	0	0	0	1
500	2	1	0	0	0	0	0	1
600	4	2	0	0	0	0	0	2
700	4	1	1	0	0	0	0	2
1000	5	5	0	1	0	0	0	6
2000	4	1	0	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

Indian Ocean

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	2	0	0	1	0	0	0	1
300	0	0	0	0	0	0	0	0
400	1	3	0	0	0	0	0	3
500	0	0	0	0	0	0	0	0
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	4	1	0	0	0	0	0	1
2000	7	2	1	0	0	0	0	3
2001+	4	1	0	0	0	0	0	1

Indian Ocean

Sternoptyx pseudobscura

Night

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	10	0	0	0	0	0	0	0
300	16	1	0	0	0	0	0	1
400	5	0	0	0	0	0	0	0
500	3	0	0	0	0	0	0	0
600	6	0	0	0	0	0	0	0
700	6	0	0	0	0	0	0	0
1000	9	2	0	0	0	0	0	2
2000	5	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Indian Ocean

Depth	Catch 0	5	10	20	50	100	100+	N
100	50	1	0	0	0	0	0	1
200	36	0	0	0	0	0	0	0
300	30	0	0	0	0	0	0	0
400	9	0	0	0	0	0	0	0
500	24	1	0	0	0	0	0	1
600	9	0	0	0	0	0	0	0
700	7	0	0	0	0	0	0	0
1000	12	4	1	0	0	0	0	5
2000	2	1	1	0	1	0	0	3
2001+	0	0	0	0	0	0	0	0

North Atlantic and Gulf of Guinea

Appendix B (Continued)

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	3	0	0	0	0	0	0	0
300	10	2	0	0	0	0	0	2
400	4	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	5	0	0	0	0	0	0	0
2000	8	2	0	0	0	0	0	2
2001+	1	1	0	0	0	0	0	1

Indian Ocean

Depth	Catch 0	5	10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0
200	7	0	0	0	0	0	0	0
300	15	0	0	0	0	0	0	0
400	39	0	0	0	0	0	0	0
500	35	0	0	0	0	0	0	0
600	14	1	0	0	0	0	0	1
700	12	0	0	0	0	0	0	0
1000	16	7	2	1	0	0	0	10
2000	12	3	0	0	0	0	0	3
2001+	0	1	0	0	0	0	0	1

North Atlantic and Gulf of Guinea

Sternoptyx diaphana

Day

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	1	0	0	0	0	0	1
200	0	0	0	0	0	0	0	0
300	1	0	0	0	0	0	0	0
400	4	0	0	0	0	0	0	0
500	1	0	0	0	0	0	0	0
600	0	1	0	0	0	1	0	2
700	1	1	0	0	1	0	0	2
1000	0	0	0	0	3	1	0	4
2000	2	1	1	1	1	0	0	4
2001+	0	0	0	0	1	0	0	1

Gulf of Guinea

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	4	0	0	0	0	0	0	0
400	14	2	0	0	0	0	0	2
500	5	4	0	0	0	0	0	4
600	1	0	0	0	1	0	0	1
700	0	1	0	0	0	0	0	1
1000	2	0	0	0	1	0	0	1
2000	1	3	0	0	0	0	0	3
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico and Caribbean

Depth	Catch 0	5	10	20	50	100	100+	N
100	3	0	0	0	0	0	0	0
200	7	0	0	0	0	0	0	0
300	9	1	0	0	0	0	0	1
400	19	0	0	0	0	0	0	0
500	20	4	1	0	0	0	0	5
600	7	0	1	2	1	0	0	4
700	4	3	0	0	1	0	0	4
1000	8	4	2	2	3	0	0	11
2000	3	1	1	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

North Atlantic

Depth	Catch 0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	3	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
400	3	1	0	0	0	0	0	1
500	0	0	0	0	0	0	0	0
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	5	0	0	0	0	0	0	0
2000	8	2	0	0	0	0	0	2
2001+	5	0	0	0	0	0	0	0

Indian Ocean

Sternoptyx diaphana

Night

Depth	Catch 0	5	10	20	50	100	100+	N
100	2	0	0	0	0	0	0	0
200	5	0	0	0	0	0	0	0
300	3	0	0	0	0	0	0	0
400	1	1	0	0	0	0	0	1
500	1	1	0	0	0	0	0	1
600	3	1	0	0	1	0	0	2
700	1	3	0	0	1	0	0	4
1000	0	2	1	3	3	0	0	9
2000	1	0	0	1	0	0	0	1
2001+	0	0	0	0	0	0	0	0

NE Atlantic (20°–40° N, 0°–30° W)

Depth	Catch 0	5	10	20	50	100	100+	N
100	3	2	0	0	0	0	0	2
200	3	0	0	0	0	0	0	0
300	4	0	0	0	0	0	0	0
400	12	4	0	0	0	0	0	4
500	2	1	0	0	0	0	0	1
600	1	0	1	0	0	0	0	1
700	2	2	1	0	0	0	0	3
1000	3	1	0	1	1	0	0	3
2000	2	4	0	0	1	0	0	5
2001+	0	4	0	0	0	0	0	4

Southern Ocean (Pacific)

Appendix B (Continued)

Depth	0	5	Catch 10	20	50	100	100+	N
100	2	1	1	0	0	0	0	2
200	0	0	0	0	0	0	0	0
300	0	1	0	0	0	0	0	1
400	0	2	0	0	0	0	0	2
500	0	2	0	0	0	0	0	2
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	1	0	1
1000	0	0	0	0	0	0	0	0
2000	0	0	0	1	1	0	0	2
2001+	0	0	0	0	0	0	0	0

Gulf of Guinea

Depth	0	5	Catch 10	20	50	100	100+	N
100	15	1	0	0	0	1	0	2
200	10	0	0	0	0	0	0	0
300	4	3	3	0	0	0	0	6
400	0	0	0	0	0	0	0	0
500	2	1	0	0	0	0	0	1
600	0	0	0	0	0	0	0	0
700	1	0	0	0	1	0	0	1
1000	0	2	0	1	0	0	0	3
2000	0	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico and Caribbean

Sternoptyx diaphana

Night

Depth	0	5	Catch 10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	8	2	0	0	0	0	0	2
300	0	0	0	0	0	0	0	0
400	4	1	0	0	0	0	0	1
500	3	0	0	0	0	0	0	0
600	6	0	0	0	0	0	0	0
700	5	1	0	0	0	0	0	1
1000	8	2	1	0	0	0	0	3
2000	3	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Western Indian Ocean

Depth	0	5	Catch 10	20	50	100	100+	N
100	30	0	0	0	0	0	0	0
200	26	0	0	0	0	0	0	0
300	19	0	0	0	0	0	0	0
400	6	1	0	0	0	0	0	1
500	18	2	0	0	0	0	0	2
600	5	3	0	0	1	0	0	1
700	0	2	0	1	1	0	0	4
1000	7	1	1	2	3	0	0	7
2000	2	0	0	1	0	0	0	1
2001+	0	0	0	0	0	0	0	0

North Atlantic (30°–45°N, 20°–70°W)

Day

Depth	0	5	Catch 10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	3	0	0	0	0	0	0	0
300	3	1	0	0	0	0	0	1
400	4	0	0	0	0	0	0	0
500	7	2	0	0	0	0	0	2
600	3	2	2	2	0	0	0	6
700	2	1	0	1	1	0	0	3
1000	2	3	2	4	1	0	0	10
2000	0	0	1	0	1	0	0	2
2001+	0	0	0	0	0	0	0	0

NE Atlantic

Depth	0	5	Catch 10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	2	0	0	0	0	0	0	0
300	3	0	0	0	0	0	0	0
400	1	0	0	0	0	0	0	0
500	2	0	0	0	0	0	0	0
600	2	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	3	1	0	1	1	0	0	3
2000	3	3	0	1	3	0	0	7
2001+	0	1	0	0	0	0	0	1

Southern Ocean (Pacific)

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The Carabid Beetles of New Guinea. Part IV. General Considerations; Analysis and History of Fauna; Taxonomic Supplement

P. J. DARLINGTON, JR.

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THE CARABID BEETLES OF NEW GUINEA. PART IV. GENERAL CONSIDERATIONS; ANALYSIS AND HISTORY OF FAUNA; TAXONOMIC SUPPLEMENT[1]

P. J. DARLINGTON, JR.[2]

CONTENTS

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[1] The author suggests that, when the four parts of *The Carabid Beetles of New Guinea* are bound together, the present part be divided, and the whole bound in the following order: general considerations, analysis, and history of the fauna from Part IV; Part I; Part II; Part III; and the taxonomic supplement from Part IV.

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ABSTRACT

This is the fourth and final part of an extended work on the Carabidae (predaceous ground beetles) of New Guinea. About 24,000 specimens from New Guinea have been examined, enough to show the general characteristics of the New Guinean carabid fauna, although many details remain unknown. Collecting done in New Guinea and in adjacent eastern Australia, the collections accumulated at the Museum of Comparative Zoology, and preparations for their study are described; working collections of New Guinean Carabidae for future use are deposited in the MCZ, the British Museum (Natural History), the Bishop Museum in Honolulu, and with CSIRO in Canberra, Australia. Localities are mapped, and those where most Carabidae have been found

(Dobodura, Wau, Mt. Wilhelm and vicinity, and the Snow Mountains) are briefly described. Then discussed are modern taxonomic methods in relation to those of the past; the continuing usefulness of types; concepts of tribes, genera, species, and subspecies; the nature of taxonomic characters; and the relative importance of secondary sexual and genitalic characters in carabid classification. Methods and procedures of second-stage faunal taxonomy (of which this work is an example) are discussed, with emphasis on the limitations imposed by time and available material.

Under "Analysis and discussion," the immense, tropical, mountainous island of New Guinea is described briefly, and its carabid fauna is described and analyzed. The taxonomic composition of the fauna is summarized. The number of species of Carabidae now known from New Guinea is 667, of which 434 occur in the lowlands, below 500 m altitude, and 376 in the mountains, above 1000 m; 161 of these species occur in both the lowlands and the mountains; and 18 additional species are unknown as to altitude. At one lowland locality (Dobodura, Papua), 217 species have been found; at one mid-altitude locality (Wau and vicinity, Northeast New Guinea, 1000–2000 m), 170 species; but numbers of species decrease sharply at higher altitudes. In size, New Guinean Carabidae are small, rarely as much as 25 m in length. The lowland fauna is bimodal in size distribution, species 2.00–2.95 and 6.00–6.95 mm long being most numerous, with a deficiency of species especially at 4.00–4.95 mm. This bimodality is a result of an apparently recent arrival in New Guinea of many small *Tachys*, which have imposed a second mode on an otherwise unimodal fauna, but the bimodality may reflect also a vulnerability of 4 to 5 mm carabids to competition with ants. The mountain carabid fauna of New Guinea is unimodal in size distribution, with the mode at 9.00–9.95 mm. Almost all lowland Carabidae in New Guinea are winged, but incidence of wing atrophy increases with altitude, reaching 95 per cent on the highest mountain tops. The causes of flightlessness at high altitudes are complex; blowing or straggling away of winged individuals is apparently unimportant, for most of the flightless species live in dense, wind-free montane forest; limitation of area on mountains, by requiring carabid populations to be dense and stable, may be the most important single factor in reducing the value of flight and inducing wing atrophy. Ecologically, the New Guinean carabid fauna at low altitudes consists of roughly one-third mesophiles (ordinary ground-living forms), one-third hydrophiles (associated with standing or running water), and one-third arboreal forms. Altitude affects the carabid fauna in several ways: in taxonomic composition (Agonini become predominant), in number of species (fewer at higher altitudes), in size distribution (see above), in wing state (see above), and in ecologic composition (relatively more mesophiles at higher altitudes), but size of individuals in specific stocks apparently does not decrease with altitude; altitude probably exerts its effects partly directly and partly indirectly, by modifying vegetation and limiting areas and habitats. Ants probably compete with and replace especially flightless mesophile Carabidae at low altitudes in New Guinea.

Under "Zoogeography," *existing* geographic patterns are first discussed, with emphasis on problems and procedures. The distribution of Carabidae in the Asia-New Guinea-Australian area is described by tribes, and the relationships of the New Guinean carabid fauna are expressed in "geographic units" (separate geographic relationships). The totals are 173 Oriental to 120 Australian units, giving a ratio of approximately 3/2 Oriental/Australian relationships; this ratio holds (roughly) for all ecologic fractions of the New Guinean carabid fauna except in opener country in southern New Guinea, where Australian elements are more numerous. Change of carabid faunas from Asia to Australia is summarized; change in ratio of Pterostichini/Agonini is most striking: these tribes are approximately equally represented in the Oriental area (Java), but Agonini are overwhelmingly dominant in New Guinea, and Pterostichini overwhelmingly dominant in Australia; this reversal of dominance has complex historical and ecologic causes. The three principal barriers to carabid dispersal between Asia and Australia seem to have been of different sorts: an old *water gap* between Borneo and Celebes (Wallace's Line), a *bottleneck* in the Moluccas caused by the relatively small size of the islands, and *ecologic barriers* between New Guinea and Australia even when there was a land connection. Although New Guinean Carabidae (and some other insects) are more Oriental than Australian in relationship, entomologists should not put New Guinea in the Oriental Region but should accept the conventional regions, perhaps adding New Guinea to the transition area (an extended Wallacea) between the Orient and Australia. Within New Guinea, some Carabidae are restricted to the western end or to the southern edge of the island (suggesting that they are recent arrivals from the Orient or from Australia), and patterns of complex differentiation of subspecies, species, and genera exist; but no special centers of speciation and no specially important barriers to dispersal at low altitudes within the island are indicated. Endemic genera are concentrated toward the eastern end

of the island; this may be a result of invasion of western New Guinea by Oriental stocks arriving from the west. Complex patterns of differentiation and local radiation occur on separate mountain ranges.

The *dispersals* that have made the existing patterns are discussed under "Dispersals and geographic origins," with emphasis on the probable importance of dominance, competition, and extinction, and on complexity. Apparent directions of dispersal of tribes, genera, and species of Carabidae represented in New Guinea are summarized. Carabid dispersal in this region is compared with that of mammals, and dispersal is related to dominance, size of insects, wings and flight, ecology, altitude, and the relative time of dispersal of different carabid groups. Conclusions in any single case are tentative, but all the cases together form a pattern of multiple dispersals mainly from Asia toward Australia. Over short distances the preponderance of eastward and southward over northward and westward movements has not been great, but over the route as a whole movements from Asia and the Oriental area to New Guinea and Australia have apparently been several or many times more numerous than movements from Australia and New Guinea to the Oriental area and Asia. Carabids have apparently been coming into New Guinea in numbers for a considerable time. There is no good evidence that arrivals have been more numerous at some times than at others; arrivals have been very numerous recently, but faunal overturns with extinctions may have obscured the evidences of earlier arrival rates. Both Oriental and Australian stocks have probably reached New Guinea at all times, but (except in the relatively dry, open areas of southern New Guinea) incoming Oriental stocks have apparently always been more numerous than Australian ones regardless of size of insects (almost all were small), regardless of wing state (almost all were winged), in all main habitats, and at all altitudes (most were lowland forms). Continual extinctions have probably been correlated with the arrivals, and the extinctions ("withdrawals") too have probably tended to begin at the Oriental end of the area and proceed toward Australia. This general history accounts for the nature of the New Guinean carabid fauna as a whole and perhaps for the distribution patterns of "mountain-hopping" groups and for Australian-American discontinuities in some cases. The trend of dispersals and extinctions from Asia toward Australia fits into an apparent world-wide pattern of evolution of successive dominant groups of Carabidae in the great, climatically favorable area of the main Old-World tropics and of successive dispersals into smaller and/or less favorable areas. And the apparent pattern of overturn of the New Guinean carabid fauna itself and the pattern of dispersal of Carabidae from New Guinea to the smaller islands to the east fit the MacArthur-Wilson theory of overturn and faunal equilibrium on islands. The New Guinean carabid fauna thus fits into and connects both world-wide and local dispersal and equilibrium patterns in a very satisfying way.

As to *evolution*, the New Guinean carabid fauna as a whole has evolved from an ancestral accumulation of relatively unspecialized, small, winged, vagile ancestors selected by dispersal across barriers and including relatively numerous species living in water-side habitats; carabids in water-side habitats tend to be vagile, and these habitats are less widely interrupted by climatic factors than rain forest is. The ancestral accumulation probably did not have a single starting time but has been an evolving continuum, added to by arrivals and subtracted from by extinctions from time to time. The existing segment of this continuum is relatively recent; the New Guinean carabid fauna is more recent in its origins than the faunas of tropical Asia, Australia, New Caledonia, or New Zealand; this may be because faunal overturn has been more rapid on New Guinea. From this changing continuum different Carabidae have evolved on New Guinea to different extents and in different ways; some multiplications of species and ecologic radiations are described. The principal general results have been to increase greatly the number and diversity of both ground-living and arboreal Carabidae in rain-forest, partly by ecologic shifts including shifts from water-side habitats to the forest floor and partly by multiplications of species, and especially to form on the higher mountains a complex alticoline fauna which, in ecology and in superficial adaptations (including wing atrophy), is like the carabid faunas of mountains elsewhere but which consists largely of genera and species apparently derived independently from lowland ancestors on New Guinea. The evolution of the mountain fauna, evolution and adaptation of separate carabid stocks, and radiation of Agonini on New Guinea are discussed in more detail. Evolutionary trends *do not* include increase of size of individuals on the island but *do* include trends toward atrophy of wings and associated structures especially on mountains, loss of setae especially on mountains, and modification of legs and tarsi especially on mountains. Parallelism or convergence have occurred among New Guinean Carabidae not only in atrophy of wings, loss of setae, and modifications of tarsi, but also in modifications of eyes, modification of body form, development of ventral pubescence (especially in diverse Agonini), development of elytral spines

(which have evolved in 40 apparently separate stocks of carabids in New Guinea), and in some elytral color patterns. These parallelisms and convergences seem to involve in different cases parallel adaptations to montane environments (wing atrophy, etc.), adaptations to specific environmental details, mechanical protection (elytral spines), mimicry (some color patterns), and occurrence of homologous or parallel mutations (some other color patterns). Occurrence of dimorphism apparently resulting from mutation among New Guinean and other Carabidae is described, and the relation of mutational changes to taxonomic characters is discussed.

In the "Taxonomic section," tribal classifications of Carabidae are briefly referred to (but no new classification is offered), and a *Taxonomic supplement* lists important new records and new species. Seventy-three new species are described, most in the tribe Agonini, and most from high altitudes. No new genera are described, but the Oriental *Physodera* and *Omobrus* (both in tribe Lebiini) are recorded from New Guinea for the first time.

INTRODUCTION TO PART IV

[1][1] *Purpose; previous parts; acknowledgments.* This is the fourth and final part of my work on beetles of the family Carabidae of the island of New Guinea. The first three parts (see *Bibliography* at end of present part) were primarily taxonomic. Part I (1962) covered the Cicindelinae (tiger beetles, which were treated relatively superficially) and the tribes of Carabidae proper from the beginning through the Pterostichini in the order of the Junk-Schenkling *Coleopterorum Catalogus* (Horn, 1926; Csiki 1927–1933). Part II (1952), which was published before Part I, covered the tribe Agonini, which is dominant in New Guinea and in which I have a special interest; my introduction to Part II went beyond taxonomy to discuss the general nature and evolution of the New Guinean agonine fauna. Part III (1968) covered the remaining tribes of Carabidae, from the Perigonini through the Pseudomorphini. The present part (Part IV) is a general summary, analysis, and discussion of the New Guinean carabid fauna as a whole, with a taxonomic supplement. This part can be divided: working copies of "The Carabid Beetles of New Guinea" can be bound with the general portion of Part IV first, then Parts I, II, and III in order, and finally the taxonomic supplement, bibliography, and statement in lieu of index of Part IV. See this statement (p. 338) for suggestions to users.

The present part actually begins with a review of material used in my work, of the history of work on New Guinean Carabidae, of localities (with new maps), and of my methods of work and taxonomic concepts. Then follow analysis and discussion of results of the work from several points of view: numbers of species, size of insects, state of wings, taxonomic composition, ecologic composition, existing geographic patterns, and origin and evolution of the fauna. Because I am a biologist (as every taxonomist should be and many are), the analysis of the fauna as a whole has been, for me, the most exciting part of my work with New Guinean Carabidae. And because I am a biogeographer, the geographic patterns and geographic histories and their significance have been most exciting of all, and I have treated them in greatest detail.

I am indebted for careful typing and other work done on the manuscript to Miss Wilmoth Peairs; for drawing done patiently under my direction to Mrs. Mary Catron and Mrs. Sarah Landry; and for support both of the work while in progress and of publication of it, to the National Science Foundation (Grant GB-12346).

[2] *Sources, disposition, and adequacy of material.* The principal sources of material used in my work on New Guinean Carabidae are listed in Part II, pp. 90–91; Part I, p. 323; and Part III, pp. 2–3. I have prepared (on cards) a consolidated list of all the museums and other institutions and all the persons from whom material has been received, and of the

[1] To avoid excessive insertions in page proof, I have assigned numbers to successive items, and shall use these rather than page numbers in cross references.

names of collectors, but the list includes more than one hundred items and seems to me not worth the space and cost of publication. The names of pertinent museums, etc., and of collectors are given under the separate species throughout my work. I need say only that I am deeply indebted to the persons there named and to the authorities of the museums and other organizations concerned. And I should add that useful material has been received, but mostly too late to be included in my work, especially from Mr. and Mrs. G. W. Cottrell and Mr. Fred Parker.

The kind of work that I have been doing with New Guinean Carabidae requires and receives international cooperation on a scale which persons who are not taxonomists do not always appreciate. I have received specimens or information about New Guinean species not only from many sources in the United States including Hawaii, but also from Canada; England, France, Belgium, Italy, Czechoslovakia, and Hungary; Japan and Java; Australia (several persons in different cities) and New Zealand; and New Guinea itself and the Solomons. And basic material or information that has formed part of the background of my New Guinean work has come also from persons in Sweden, Germany, Switzerland, and India.

In general, borrowed material has been returned to the sources from which it was received, with duplicates kept for the Museum of Comparative Zoology (MCZ). In a few cases additional important specimens, including holotypes, have been deposited in the MCZ for safekeeping. I am especially indebted to Dr. J. J. H. Szent-Ivany for the Department of Agriculture, Port Moresby, and to Dr. R. W. Hornabrook for permitting holotypes from their material or from material in their charge to be deposited in the MCZ. This arrangement safeguards irreplaceable specimens and makes them more easily available to specialists, and is a real contribution to future work on the carabid beetles of New Guinea.

On the other hand, duplicates of my own material have been widely distributed. I have tried especially to build up the best possible working collections of New Guinean Carabidae in the British Museum; the Bishop Museum in Hawaii; and with the Commonwealth Scientific and Industrial Research Organization (CSIRO), in Canberra, Australia. For further discussion of the place of types and of working collections of specimens in modern taxonomy see [6, 7].

The number of specimens of Carabidae proper (excluding Cicindelinae) actually recorded from New Guinea in Parts I–IV is about 22,500. In addition I have seen perhaps 1000 or 2000 additional specimens from New Guinea without counting them (an exact accounting has not seemed worth the trouble), and of course I have seen many thousands more from the Oriental Region and from Australia (see Part I, pp. 325–328). Most of the specimens from New Guinea were collected during or after the war, and most of them have exact localities, often altitudes, dates, and names of collectors. About 8000 of the New Guinean specimens were collected by myself (see [3]). I have at least a rough idea of the habitats of most of the species that I obtained, and some specimens collected by other persons have indications of habitat. Many of the recently collected specimens were taken at light; these probably flew, at night. However, there is often no way of knowing whether individuals taken at light came from forest or grassland or swamps, or whether they lived on the ground or were arboreal.

All this material is adequate to show the general nature of the New Guinean carabid fauna as a whole. The material probably includes most existing primarily lowland species and good samples from a few mountains, although hundreds of mountain-living species localized at different levels, on different ranges, and on different peaks

of the same ranges surely still remain to be discovered. In all, enough species are known from enough material to allow significant statistical analysis of the fauna as a whole. But the material of most single species is not sufficient for statistical study of either individual or geographic variation. Much more collecting and much more study will have to be done to make known the variation and geographic distribution of most species even at low altitudes, and the mountain-living species are much less well known. And, although so much still remains to be done on the structure, variation, and distribution of the species, much more remains to be done in the insects' biology. About all that is known of the ecology even of the best known lowland species is their gross habitat and whether or not they fly to light, and not even this much is known of most high-altitude species. And the life histories of most New Guinean Carabidae are wholly unknown, excepting only *Pseudozaena* and *Morion* (Gressitt, 1953) and a few genera and species of "Truncatipennes" which occur also in Japan and for which Habu (1967) gives biological notes.

[3] *Preparation for work on New Guinean Carabidae; my collecting.* Previous work on Carabidae of New Guinea is briefly described in Part I, pp. 324–328. Points emphasized and worth repeating are the small amount of work done on actual New Guinean specimens in the past, and the importance of work done on Carabidae of adjacent areas, especially by T. G. Sloane on the Australian fauna and by H. E. Andrewes on the fauna of the Oriental Region including the western part of the Indo-Australian Archipelago. Sloane's and Andrewes' collections (which I have seen and studied) and the descriptions and revisions published by these two persons are the basis for study of the relationships and history of the New Guinean carabid fauna.

My own interest in and work on Carabidae of the Oriental Region and Australia as well as of New Guinea, and the collections accumulated at the Museum of Comparative Zoology, are briefly described too in Part I, pp. 325–328. As a result mainly of my own activities beginning in 1931–1932 (when I was a member of the Harvard Australian Expedition), the MCZ now possesses a good working collection of Carabidae not only from New Guinea but also from both major source areas (Oriental and Australian) from which the New Guinean fauna has been mainly derived.

Although my collecting is summarized in Part I (pages cited above), a few additional details are worth giving here. In collecting around Dobodura I was first struck by the very slow rate at which species accumulated. The first day I found, I think, only three or four species, and few individuals. The next day I found perhaps two or three additional species. And so forth. But when I came to sort out the species and study them at the MCZ, I found that I had obtained 217 species at this one diverse but strictly lowland locality! The slowness with which species accumulated was, I think, due only partly to a temporary physical handicap of mine. It was probably due partly to the fact that, although species are diverse in the tropics, many have sparse populations and (even in relatively small, ecologically homogeneous areas) patchy distributions (Wilson, 1958).

My impression is that populations of Carabidae tend to be most sparse and most scattered on the rain-forest floor. Collecting in the leaf litter and loose soil on the floor of rain forest does in fact call for patience and ingenuity if the diverse fauna which lives there is to be adequately sampled. Old-fashioned sifting handles too little material to yield an adequate sample of the thinly dispersed fauna in a short time. Berlese funnels are better and are indispensible for collecting some insects, but are probably still too slow to obtain Carabidae in adequate numbers—and I had no Berlese equipment.

The method that I did use, and that I

think is most effective in rapid sampling of rain-forest-floor Carabidae, is what I call washing or drowning. It involves raking or scraping up large quantities of leaf litter and loose surface soil and throwing them into still water where the light is good. The debris is spread out on the water surface, thoroughly wetted and gently stirred, and perhaps stirred again at intervals. The Carabidae, of course, came to the surface of their own accord, and usually run across the floating debris toward the shore, where they are picked up by the waiting collector. Some take flight and must be caught the instant they appear. Others run down the floating debris again if they are alarmed on the surface. And some, especially some fossorial forms, come to the surface only after considerable delay. Sometimes the collecting is complicated by small birds and lizards, which wait close by and make dashes for moving insects.

The collector who uses this method for the first time is likely to be disappointed in it. It requires judgment and experience in selecting the right places and in raking up debris in the right way. However, properly used, it yields good collections even from material scraped from ordinary, thin, rain-forest leaf litter. And the yield is sometimes multiplied in washing out piles of leaves that have been concentrated by some natural means, for example under the head of a tree that has fallen and from which the dead leaves have dropped thickly on the ground. Flash floods in the rain forest, which wash masses of leaves and other debris together, are best of all, provided the collector can work them immediately, while the water is rising or at least before it starts to fall, before the Carabidae have had time to redisperse and before ants and other predators have had time to decimate them. A flash flood at Dobodura, which brought down the bank of a gully and dammed water back over a piece of flat ground in heavy rain forest, gave me the best collecting I had in New Guinea. In it, I found (I think) all my *Odontomasoreus humeralis* (Part III, p. 76) at Dobodura, all my *Nototarus papua* (Part III, p. 186), my only specimen of *Colasidia papua* (present part, *Tax. suppl.*), probably two of my three specimens of *Pheropsophus catulus* (Part III, p. 328), and series of other ground-living carabids that I rarely found at other times.

One additional note: at Dobodura, as elsewhere in the tropics, virtually no Carabidae were found under stones on the ground. Under stones is, of course, where northern collectors first look for Carabidae, and failure to find them there in tropical rain forests has perhaps contributed to the idea that Carabidae are scarce insects in the tropics. But the Carabidae are there in numbers and diversity—just not under stones (see following paragraph).

On the Bismarck Range and Mt. Wilhelm [5] my time was so limited that I got only a skimpy sample of the carabid fauna. I was impressed by the fact that at these altitudes (*c.* 2000 m and higher), Carabidae did commonly occur under stones (cf. preceding paragraph). In fact some of the same species that in my experience were *never* found under stones at low altitudes were found there in the Waghi Valley on the Bismarck Range. It therefore seems not that the requirements of tropical Carabidae are different from those of temperate ones, but that the microclimate or microhabitat under stones in the full tropics is somehow inhospitable to most Carabidae.

Of my collections made outside New Guinea (Part I, pp. 327–328), the most important is a comprehensive collection of wet-forest Carabidae made along the whole eastern edge of Australia, from northern Cape York to southern Tasmania, during 19 months in 1956–1958 (Darlington, 1960).

[4] *Basic literature.* Work done on any fauna is carried over from generation to generation in the form of collections, publications, and sometimes unpublished manu-

scripts. Collections of New Guinean Carabidae available for future work are noted elsewhere [2]. Publications and manuscripts essential to or resulting from work on New Guinean Carabidae are listed in more detail in the *Bibliography* (pp. 334–337) and under many of the species treated in Parts I–IV, but the more important items may usefully be summarized here.

Basic to work on Carabidae in any part of the world are the Junk-Schenkling *Coleopterorum Catalogus* (Horn, 1926; Csiki, 1927–1933) and the *Zoological Record*. The former (often called the "Junk Catalogue") lists all Carabidae of the world up to within a year or two of the dates given, with very few omissions and not many errors of citation, and with bibliographies and indications of distribution, both sometimes incomplete. This work is still available from W. Junk, Publisher, 13 van Stolkweg, The Hague, Netherlands. The annual volumes of the *Zoological Record* list additional papers and new genera and species published from year to year, and enable students to compile preliminary bibliographies and preliminary faunal lists.

Basic works on the Carabidae of the Oriental Region and Indo-Australian Archipelago include H. E. Andrewes' papers (see Part I, p. 325) and especially his (1930) "Catalogue of Indian Insects, Part 18, Carabidae," which in many genera lists all species known from the Indo-Australian Archipelago including New Guinea; Louwerens' papers, especially his (1953) revision of Oriental *Colpodes;* studies by the late Arnost Jedlicka and by Akinobu Habu, especially their long papers on Oriental "Truncatipennes" (*see Bibliography*); and work now in progress by Shun-Ichi Uéno especially on Trechini. Also useful to future workers should be my manuscript list of Carabidae of the Indo-Australian Archipelago including New Guinea, based on the *Coleopterorum Catalogus* and the *Zoological Record*, but amplified and brought up to date. This manuscript is not prepared for publication, but I expect to deposit Xerox copies of it in the Department of Entomology at the British Museum, in the Bishop Museum in Honolulu, and with CSIRO at Canberra in Australia. The original manuscript will, of course, be kept at the MCZ.

Basic work on Australian Carabidae has been done principally by T. G. Sloane (see Part I, pp. 324–325), who published also two short papers (1907) on New Guinean species. Work done and being done on Australian Carabidae by B. P. Moore should also be followed by those interested in the New Guinean as well as the Australian faunas. My own papers on certain groups of Australian carabids may be useful in some cases, especially since they are related to my New Guinean work; papers on my Australian collecting localities (1960) and on transition of wet-forest carabid faunas from New Guinea to Tasmania (1961) may be especially useful. My manuscript list of Australian Carabidae, based again on the "*Junk Catalogue*" and *Zoological Record* but amplified by search of all Sloane's papers and much other literature, may save time for later workers; a copy of it will be deposited with CSIRO at Canberra.

Works on Pacific Carabidae that should be considered in studies of New Guinean species include H. E. Andrewes' (1927) paper on Carabidae of Samoa; E. C. Zimmerman's "Insects of Hawaii," especially his introductory volume (1948) and his projected volume on Hawaiian Carabidae; and other work done and being done at the Bishop Museum or on Bishop Museum material, including my paper (1970) on the Carabidae of Micronesia.

As to New Guinea itself, my "The Carabid Beetles of New Guinea," of which the present paper is Part IV, coordinates earlier work and should be the basis for future work on New Guinean carabids, especially for third-stage taxonomic study of selected groups (see Part I, pp. 328–330). Three volumes that will be important

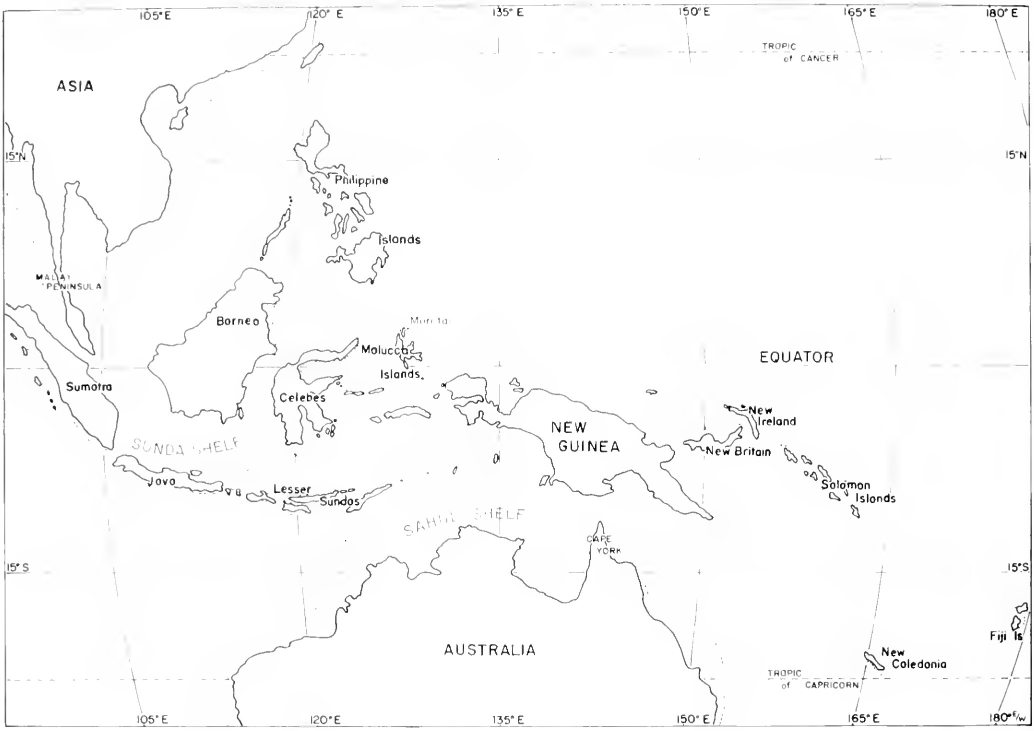


Figure 1. Map to show relation of New Guinea to Asia and Australia. Broken lines (at c. 100 fathoms depth) show approximate limits of continental shelves and some other areas of shallow water which were probably land at times in the Pleistocene.

to entomologists working on New Guinean Carabidae and other insects are in press or are planned by J. L. Gressitt and J. J. H. Szent-Ivany (joint authors). The first (now published, 1968) is a bibliography of New Guinean entomology. The second, now being planned, is a history of entomological exploration in New Guinea, with a list of localities. And the third, also being planned, is on the environment of New Guinea from an entomological standpoint. (This information is from a letter from Dr. J. L. Gressitt dated December 26, 1967.)

[5] *Localities.* Ideally, I should like to map all New Guinean localities at which Carabidae have been collected, but this has proved beyond my power. I can, however, present the following new maps, prepared by Miss Sally Babb (now Mrs. Joseph Landry) under my direction. Figure 1 is a small-scale orthographic map designed to show the relation of New Guinea to other land areas from southern Asia to northern Australia. Figure 2 is a map of New Guinea as a whole showing general features of the island, some localities, and outlines of limited areas which are mapped in more detail. And Figures 3–5 are more detailed maps of parts of New Guinea in which important carabid localities are too numerous to show on Figure 2. Many New Guinean localities are spelled in different ways by different authorities, but I cannot list alternative spellings here. Some localities are put in slightly different places on different maps and by different gazetteers; some margin of error should therefore be allowed for in using my maps. And where detailed localities are too crowded to distinguish, I have shown only general

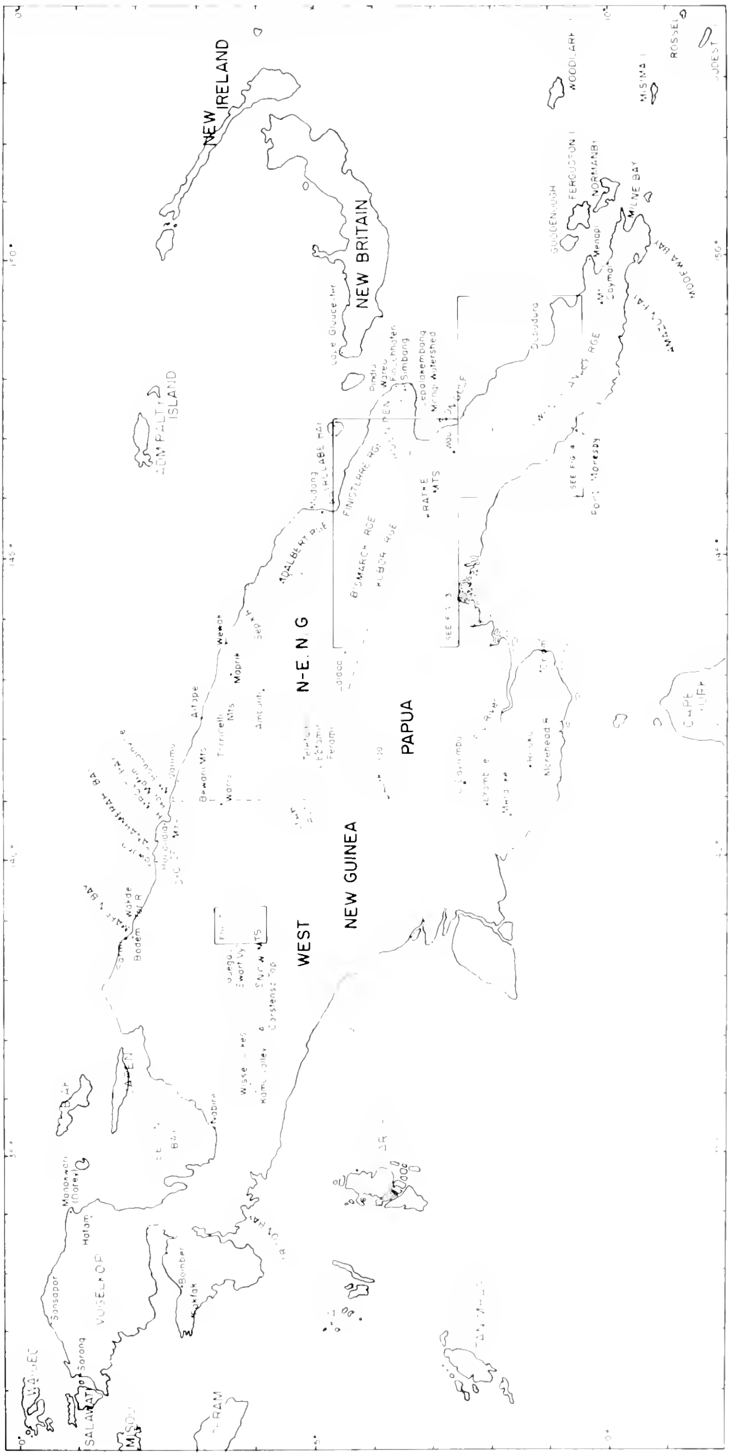


Figure 2. Map of New Guinea, showing general features, some carabid localities, and outlines of areas mapped in more detail in Figs. 3–5.

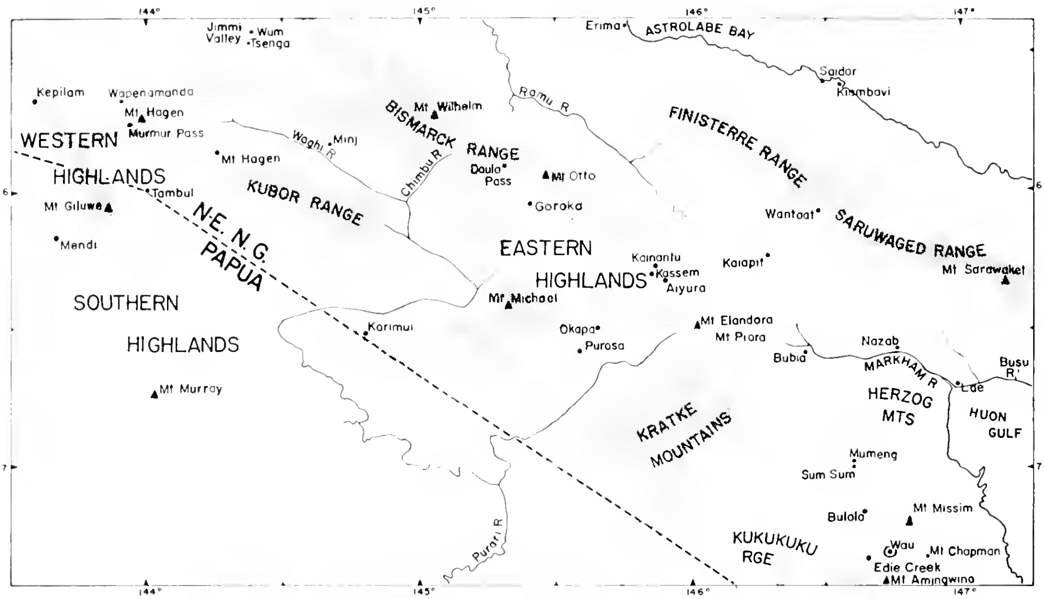


Figure 3. Map of part of eastern North-east New Guinea and adjacent corner of Papua, showing especially carabid localities. High mountain areas (above c. 2500 m) are shaded, but their limits are only approximate.

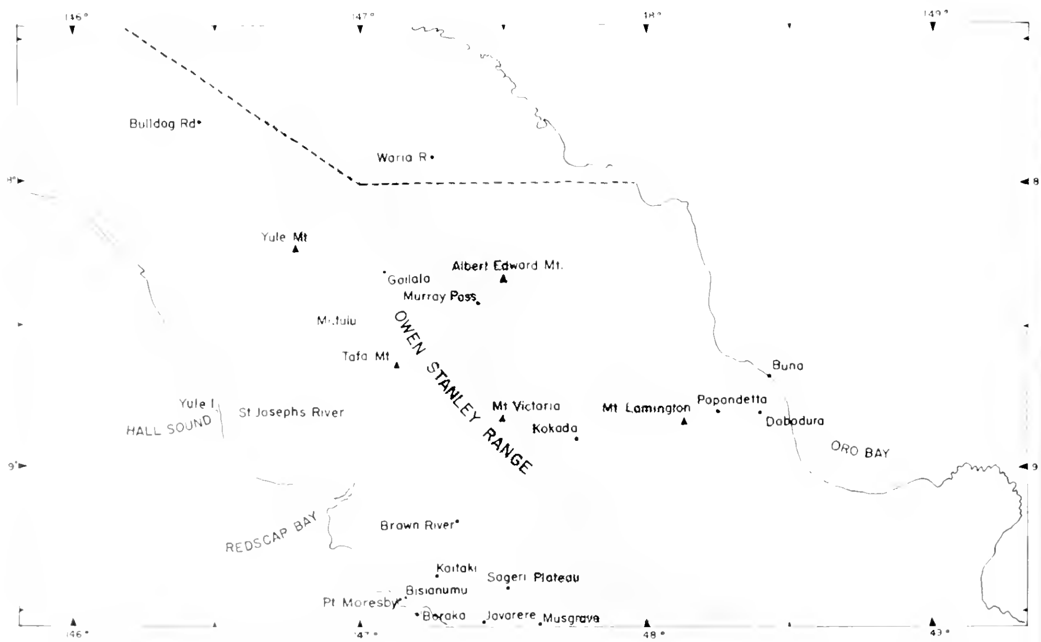


Figure 4. Map of part of eastern Papua and adjacent corner of North-east New Guinea, showing especially carabid localities. High mountain areas (above c. 2500 m) are shaded, but their limits are only approximate.

areas: e. g., Wissel Lakes, Cyclops Mountains, Sepik River, and Waigeo Island.

The best map of New Guinea for general purposes is (I think) the current set of USAF Operational Navigational Charts (see *Bibliography*). For spellings of well-known islands, mountain ranges, and localities I have usually followed *Webster's Geographical Dictionary*. To find less-known localities in New Guinea I have used primarily the blue, paper-bound gazetteers of the United States Board on Geographic Names (see *Bibliography*). Also very useful is the "Bishop Museum List of New Guinea localities, 1966," which is a provisional list of localities at which collections have been made by Bishop Museum entomologists and by some other persons. This will be replaced by Gressitt and Szent-Ivany's book (referred to above) on entomological exploration and localities in New Guinea. A shorter list of localities, which is useful because it covers collecting done by soldiers during the war, is in Arthur Loveridge's paper on New Guinean reptiles and amphibians (1948: 310–314).

Sources of information about the localities of important carabid collectors include a summary of Miss L. Evelyn Cheesman's work in New Guinea, in Charles Barrett's *The Pacific*, pp. 63–65. Miss Cheesman spent two and a half years (chiefly in 1933–1934) in Papua, mostly on the Owen Stanley Range and in the mountainous area southwest of the Albert Edward Complex. Then she was about a year (chiefly in 1936) in the Cyclops Mountains and near Lake Sentani (vicinity of Hollandia). And later (in 1938–1939) she collected extensively in Waigeo and Japen Islands, and briefly in the Torricelli Mountains. Most of her localities will be found in the Bishop Museum list of localities referred to above.

A source of useful information on limited areas in New Guinea is the series of reports of the Archbold Expeditions in the *Bulletin of the American Museum of*

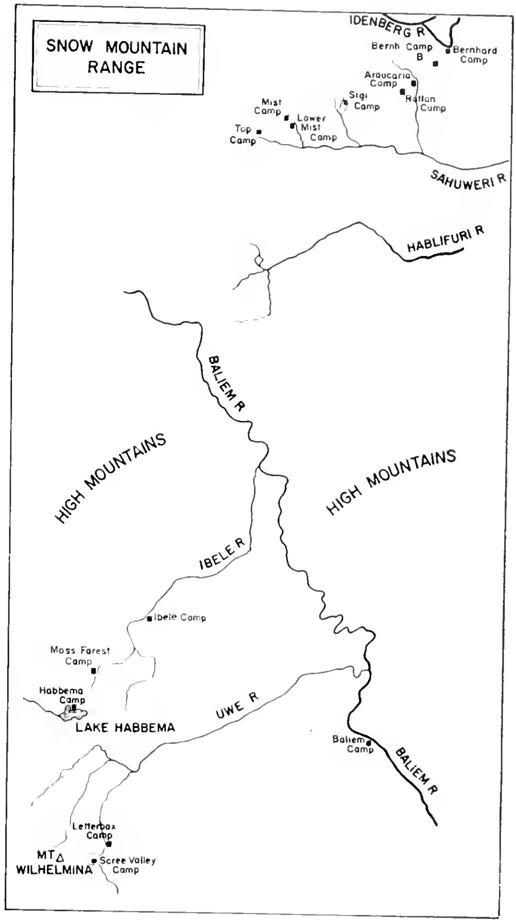


Figure 5. Part of the Snow Mountain range, West New Guinea, showing especially the localities at which Carabidae were obtained by the Netherlands Indian-American (3rd Archbold) expedition of 1938–1939. Redrawn from Toxopeus, 1940.

Natural History, including items by L. J. Brass (1941 and 1964) on the expedition to the Snow Mountains and on an expedition to Mt. Wilhelm and vicinity and to the Lae-Edie Creek area (vicinity of Wau). Localities of the Archbold Expedition to the Snow Mountains have been published separately by Toxopeus (1940).

See Gressitt and Szent-Ivany (1968) for references to accounts of New Guinea collecting by Biró, Cheesman, D'Albertis, Gressitt, MacLeay, Maindron, Székessy

(concerning Biró), Szent-Ivany, Toxopeus, Wallace, Wilson, and others.

I should at this point say something about altitudes. Exact or approximate altitudes of many localities are given on maps, or in the Bishop Museum list, or on locality labels on specimens. However, even modern altitude determinations are sometimes inaccurate, and the altitudes given on maps are not necessarily the altitudes at which collecting has actually been done. The risk of error is greatest in the case of material collected long ago. We are not justified in assuming that old specimens labeled (for example) Sattelberg came from the immediate vicinity of the town or from the same altitude. They may have been collected many miles away and many hundreds of meters above or below the altitude of the town itself. I have usually omitted old locality records in discussing the distribution of New Guinea Carabidae in relation to altitude [26].

Several localities where especially important collections of Carabidae have been made are worth separate notice here.

Dobodura and vicinity (which includes Oro Bay), Papua, are briefly described in Part I, pages 325–326, and a few more details are given in the present part [3]. It is a strictly lowland area; my collecting there probably did not extend above 200 meters altitude. But the area is otherwise diverse: habitats within easy walking distance of Dobodura included heavy lowland rain forest, various kinds of second growth, grassland, swamp margins, and the banks of streams including a small river, sluggish brooks, and rapid brooks in foothill topography. Important lowland habitats missing in this area were, I think, only special coastal ones, those associated with really large rivers, and those confined to the open eucalyptus country of southern New Guinea. My collection of Carabidae from Dobodura comprises 217 species [19] and more than 4,000 specimens.

A second very important locality or group of localities is Wau, with Edie Creek, Mt. Mis(s)im, Mt. Kaindi, etc., in the Morobe District of North–east New Guinea. This is a diverse, mid-altitude area, indicated in Figure 3. Of this area, Gressitt (letter of December 26, 1967) says, "A description of the environment just above Wau is found on pages 182–185 of Volume 127 (1964) of the Bulletin of the American Museum of Natural History, by Brass. This is under the heading 'Kaindi, Morobe District.' Part of the area described in that section is what we call Edie Creek. And most of our material labeled Kaindi is from just above the area described in that section. Wau proper is just below these areas, at the foot of Kaindi, around the lower part of the Edie Creek Road. Several of our localities like Kunai Creek, Nami Creek, Delias Creek, are along the Edie Creek Road above our field station.

"There is a tremendous range of vegetation types from the bottom of the Bulolo Gorge just below Wau to the top of Mt. Kaindi and to the top of Mt. Missim, the higher mountain on the north side of the Valley (from which MCZ has some old material). Among the main differences of the lower part of the valley with the area described in Brass' paper is the fact that *Araucaria* is dominant in many parts of the valley to just about the level of our field station. Also, palms and many other tropical trees are in the lower forests, extending above the station. In Wau Valley itself, there is a great deal of coffee grown. Also, a lot of the *Araucaria* has been cut and pure stands of both species have been planted after destruction of the remaining native forest. Still, there are extensive areas under natural vegetation. And more particularly so going higher on the two mountains."

Brass's (1964) paper should be referred to for further information about the Wau area, especially its vegetation, and for photographs. Carabidae collected between 1000 and 2000 meters altitude in this area now number 170 species, and 35 additiona

pecies have been found in the vicinity ither at higher or at slightly lower alti- udes. This is an outstandingly fine col- ection—a notable accomplishment by the 3ishop Museum entomologists using their ield station at Wau.

My brief visit to and the collection made n the Bismarck Range and Mt. Wilhelm in)ctober 1944 are briefly described in Part , pages 326–327, and Part IV (the present art) [3]. A sketch map of my route to At. Wilhelm is in Part I, p. 326, and resent Figure 3 shows the position of the nountain in relation to localities at which ther collectors have obtained Carab- dae more recently. The altitude of Mt. Vilhelm, previously considered to be about 5,400 ft., is now considered to be about 4,600 ft. (*c.* 4450 m). Specimens collected y me in this area bear three different abels. Those from the lower, more open ountry are labeled "Chimbu Valley, Bis- narck Range, 5,000–7,500 ft.," and were aken in the densely inhabited valley, most f which has been highly modified by man, nd which is now largely grass or gardens, lthough very limited habitats including he edges of small streams and of the Chim River are still natural. Specimens taken in he montane forest, which changes from ain forest to moss forest with increasing ltitude, are labeled "Mt. Wilhelm, Bis- narck Range, 7,000–10,000 ft.," and were aken on the ground in the forest, mostly nder stones and logs or beside running vater. Finally, specimens taken above the orest line, in "subalpine" habitats, are abeled "Mt. Wilhelm, Bismarck Range, bove 10,000 ft.," and were taken either n the ground under various kinds of cover ncluding tussocks of grass, or beside small treams in tussock-grass country, or (*Macu- agonum altipox* only) in a grass tussock. 'or further information and photographs f the Bismarck Range and Mt. Wilhelm, ee Brass (1964) and Brookfield (1966: 79–183). Brookfield (pages cited) sum- narizes the geology as well as the egetation of the area. This range (like many of the other mountains of New Guinea, I think) is described as "a recent fold-structure which was uplifted in a series of stages culminating in the late Tertiary," with complexly faulted strata which include limestone.

The localities in the Snow Mountains, West New Guinea, at which L. J. Toxopeus obtained his fine collection of Carabidae, are briefly described by him (1940), with altitudes and very brief descriptions of the vegetation. I here reproduce Toxopeus' map, somewhat simplified (Fig. 5). His localities cover virtually all the important montane habitats from cultivated valleys below 2,000 m, through various types of forest at increasing altitudes, to "alpine" areas above timberline. The highest altitude at which collecting was done was 4,250 m, but "results were few" this high up.

Evidence that "Dor(e)y" labels have been wrongly placed on many Carabidae, collected by Alfred Russell Wallace, that probably really came from Celebes or the Moluccas is given in Part I, pages 330–331, and Part III, page 5. Wallace did collect at Dor(e)y in West New Guinea, but he or someone else evidently labeled as from there many specimens which really came from other islands.

POLICIES AND METHODS

[6] *Modern taxonomy.* "Modern taxonomy" means different things to different persons. To me, it means taxonomy as practiced now, and it is worth considering what the policies and methods of taxonomy now are. In general, I think modern taxonomy, as compared with the taxonomy of one or two generations ago, is more carefully calculated to reflect real situations in nature and more carefully designed for intelligibility and utility. Modern taxonomy also employs new techniques and new procedures appropriate to the material and purpose of each particular piece of taxonomic work, but the new techniques and procedures are for the most part added to,

not used in place of, the procedures of the past. Taxonomic work has therefore become increasingly complex and difficult, but also more precise and more useful. See Mayr (1969) for detailed discussion of the principles and procedures of this kind of work. And see the volume on *Systematic Biology* published by the National Academy of Sciences–National Research Council (1969) and current numbers of the journal *Systematic Zoology* for discussion of various aspects of modern taxonomy.

Within my general definition several levels and many different methods of taxonomy are possible. My methods are specifically those of second-stage faunal taxonomy as described in Part I, pages 328–330, limited by the amount and kind of material available from New Guinea and by the amount of time I have been able to devote to the project.

The methods I use are essentially subjective: comparison of specimens, detection of similarities and differences, and reaching of conclusions based primarily on personal judgment and experience rather than on statistical analyses or other objective tests. I have tried to make my taxonomy conform to phylogeny and reflect the existence and variability as well as the interrelationships of populations in nature. For practical purposes, Carabidae have no fossil record. Their phylogenies must therefore be deduced, and taxonomists are sure to make mistakes about them. Nevertheless the results of the kind of work I am describing have a gross phylogenetic reality perhaps best demonstrated by its utility: zoogeography based on this kind of taxonomy makes sense, and it would not be expected to make sense if the phylogenetic basis of the taxonomic work were seriously in error.

The methods I use are, of course, essentially the same as those used by Darwin and by a multitude of taxonomists before and after him, although his predecessors were not aware that their classifications reflected phylogenies. The method is fundamentally simple. Different kinds of animals (or of plants) are compared; characters they share are assumed to be primitive (unless there is evidence to the contrary); and characters by which they differ are assumed to be derivative and to indicate divergent lines of evolution. Of course use of these basically simple criteria can become very complex in practice, as a result of parallelism and convergence, loss of structures, and other complexities and irregularities in the phylogenies of complex groups. In fact, classifications almost always extremely oversimplify phylogenies. This is a necessary result of the complexity of evolution, and it does not spoil the usefulness of the classifications, if the latter are consistent with phylogenies. In modern terms (Mayr, 1969) classifications like mine are phyletic but not cladistic, and of course not phenetic. In a few cases, especially among some Agonini that have radiated on New Guinea, I have been unable to recognize phyletic lines and have therefore temporarily classified the insects by grades—my "genera of convenience" [9] are of course grades.

Hennig (various publications, culminating 1966) and others (notably Brundin 1965; 1966) have proposed a formal system of "phylogenetic" (cladistic) systematics. Their methods are not fundamentally different from those that have always been and still are used by most taxonomists. The cladists, like the rest of us, look for similarities and differences among the organisms they study, and make subjective judgments about relationships and divergences and about primitive and derivative characters on the basis of what their comparative studies show. Unless their subjective judgments are of a different order from other persons' judgments (of course they are not!), their fundamental methods are no different from and no better than other persons' methods. It seems to me extraordinary that they do not seem to realize this fact! However, the cladist

then force their classifications to fit an inflexible hierarchy of taxonomic categories determined by the (supposed) sequence of branching points of the phylogenies they have worked out by conventional means. The new methods (so far as they are new) and the new terms are (I think) not useful but merely make taxonomy rigid and unadaptable. Among the assumptions that I object to in "cladism" are that evolution proceeds at a fairly constant rate, that phylogenies are fairly regular successions of dichotomies which the cladists can reconstruct and date even without a fossil record, and that primitive ("plesiomorphous") characters are rather easy to recognize. Criteria of primitiveness have, in fact, been known since Darwin, but are often more difficult to use than Hennig and Brundin seem to realize. Even more dubious is the assumption by at least some cladists that there is a simple correlation between primitiveness and geographic distribution and that the most primitive existing forms of any given group persist at the group's place of origin. Do persons who make this assumption suppose that primitive stocks cannot disperse, or that evolution is suspended at places of origin? Among Carabidae this whole concept is made ridiculous by the fact that possession of wings is primitive and atrophy of wings derivative, but that it is the primitive (winged) stocks that do in fact disperse most readily. Of course the matter is really much more complex than this, but I cannot take space to discuss it further here. In the present work I reject the idea that the places of origin of widely distributed groups of Carabidae are revealed by the present occurrence of primitive forms. Other methods of tracing geographic histories are briefly discussed in Section [74]. In general, I think taxonomists using less arbitrary methods can do as well or better than cladists in fitting their classifications to phylogeny and in interpreting geographic patterns. For a more detailed practical criticism of Hennig's and Brundin's ideas and procedures, see Darlington, 1970a.

Numerical taxonomy is not adapted to the kind of work I do. It requires more and better material and much more time than I have. And I would not use it in any case unless I thought (I do not) that the results would be more useful than the methods I do use. Of course some numerical taxonomists do not even pretend that their classifications are phylogenetic.

To return to modern taxonomy, it is worth some further consideration of what present-day taxonomy is, without the artificial rigidity of Hennig's system and without the aberrations of numerical taxonomy.

One important characteristic of modern taxonomy is that very much more material is used than was usually available in the past. For example, when Sloane (1907) wrote on Carabidae from New Guinea, he had only 30-odd specimens from that island and New Britain, while I have had about 24,000 specimens from New Guinea alone [2]. In fact I have had to cut off the flood of incoming material in order to finish my work at all!

Another way in which modern taxonomy often differs from that of the past is that taxonomists themselves are more likely to have collected substantial amounts of the material they study. For example, Sloane was never able to collect in New Guinea, and Andrewes, who worked so extensively on the Carabidae of the Oriental Region and Indo-Australian Archipelago [4], collected only in India and only a handful of specimens there, while I have been fortunate enough to collect about one-third of the carabid specimens I have studied from New Guinea, including individuals of more than half the species. The basing of work on large amounts of material, substantial parts of it collected by the taxonomists themselves, gives the latter first-hand knowledge of populations in nature and of the variation, ecology, and distribution

of species, and surely should contribute to realistic, useful taxonomy.

Modern taxonomy, even the nonnumerical kind, does include methods that (added to the old methods) improve the procedures and results of taxonomic work. For example, statements of proportions are now usually based on careful measurements made under the microscope. Proportions, such as the relative widths of head and prothorax and the ratio of width to length of prothorax, were often simply estimated or guessed at by taxonomists working on Carabidae two or three generations ago. New and useful kinds of characters have been found and utilized in carabid taxonomy, for example presence or absence of specific setae on many parts of the body, the patterns of surface microsculpture as seen under the microscope at 50 × or 100 × magnifications, and the state of the inner wings. Use of genitalic characters too has advanced our understanding of the natural classification and phylogeny of Carabidae, although I have not been able to make much use of genitalic characters in my work on New Guinean carabids (see [13]).

One other characteristic of modern taxonomy seems to me to be that emphasis has shifted from descriptions to actual specimens, or from words to animals. Descriptions cannot be made full enough and accurate enough to satisfy later workers. Each generation of taxonomists must see the actual specimens used by earlier generations, and I think the tendency now is, or should be, to make descriptions short, but of course explicit and carefully calculated, and to make specimens widely available. This is facilitated by the very large amount of material now often available (see third paragraph above). I have tended to make descriptions shorter and shorter during the course of my work, and I have also varied their length according to the number of specimens that I have for distribution. Relatively long descriptions are most likely to be needed in the future when only one specimen of a species is known, even though unique types are now loaned more often than they used to be. I should add that, in faunal works on remote areas like New Guinea, descriptions of species based on single specimens are still often necessary. To put off the work until more material becomes available might well mean that the work would never be done. And of course the chance of more material being obtained is greatly increased when descriptions are published, so that collectors can know what species to look for in what localities. To return to more ordinary cases, I think that descriptions should be short, partly because complete descriptions are impossible, partly because very long ones waste time both in the writing and in the using, and partly because the cost of publishing very long descriptions is excessive. But, to compensate for the shortness of descriptions, I think that it is an important function of modern taxonomists to distribute working sets of specimens and to tell readers where the sets are. Working sets of my New Guinean Carabidae are being distributed as described [2].

[7] *Types.* In this context, of increasing emphasis on animals rather than descriptions, type specimens remain decisively important. They are necessary to stabilize nomenclature. (If names of genera and species have not been stabilized, this is more often a result of bad judgment by taxonomists than of failure of the existing code of nomenclature—but this is a delicate matter which cannot be adequately expounded here.) And, more important, types (which are animals warranted to be properly identified) are the best means of assuring that in the future biologists will know (or can know, if they want to take the trouble) what animals biologists are talking about now. Types or equivalent "voucher specimens" are therefore as important to ecologists, behaviorists, geneticists, and physiologists as to taxonomists.

So far as New Guinean Carabidae are

concerned, the great collections of older types are in the London and Paris Museums, while the MCZ possesses the largest collection of more recent types of these particular beetles.

Taxonomists who designate and use "types," and who sometimes have to work with limited material or single specimens. are sometimes accused of being "typologists," but I think this is a confusion of terms. The original typologists were Greek, and they dealt in abstractions rather than reality. Their types were idealized perfections never attained in reality. But the types of taxonomists are real specimens that can be put under the microscope and described, and put under it again and the details checked. I do not know any taxonomists now who really treat types as abstractions or who do not understand that types are individuals which represent populations but which do not show all the populations' characters. If there are typologists in taxonomy now, I think they are the mathematical biologists who take limited samples of populations and from them derive mathematical formulae intended to represent the characteristics and limits of the whole populations. The formulae *are* abstractions which cannot be wholly correct. Samples are not likely to show all the variation of whole populations. And formulae based on samples are often extrapolated unjustifiably, as if variation were continuous, although in fact much variation is discontinuous. Mathematical typologists produce idealized models which are useful for reference but which should not be confused with reality.

[8] *Taxon concepts: subfamilies and tribes.* My concepts of subfamilies, tribes. genera, species, and subspecies are worth brief discussion, not so much to defend them as because readers should know my usage in order to understand my taxonomy.

In the case of subfamilies, I have followed the *Coleopterorum Catalogus* (Horn. 1926; Csiki, 1927–1933) as a matter of practical convenience, because this is the latest arrangement that covers the Carabidae of the whole world. However, the great subfamilies Carabinae and Harpalinae are surely unnatural (polyphyletic) and should be (and by some recent authors have been) broken up.

The tribes now recognized [18] are, I think, mostly natural, although many details are undecided. The number of tribes to recognize is a matter of utility and intelligibility rather than of fact. It seems to me that the number should be small enough, and the names and limits of the tribes stable enough, so that most of them will be recognized by most students of Carabidae everywhere. My use of tribes is therefore conventional, approximately the same as that of Andrewes, Sloane, and Ball [101]. Jeannel (1940–1941) has, I think, split tribes too much. He has divided what most of us call the single family Carabidae into about 50 separate families, many of which are further divided into subfamilies and tribes. I do not mean that the splitting is wrong in itself. The old tribes can and should be subdivided when natural characters can be found to do it. But the subdivisions can be treated as subtribes or groups of genera. This allows specialists to refine classifications without imparing their intelligibility.

[9] *Genera.* The genus is not a naturally limited entity. It should conform to phylogeny when possible (see "genera of convenience," below), but natural (phylogenetic) genera can be broad or narrow, and the decision how broad to make them is often a matter not of fact but of intelligibility and utility. In general, I think genera should be broad, with names and limits as stable as increase of knowledge will allow, but large genera can often usefully be divided into subgenera.

For example, among tiger beetles (Cicindelinae) I think it is useful to recognize the immense genus *Cicindela* in the old-fashioned sense (see Part I, pp. 340ff). This genus then includes about half the existing tiger beetles, and it is world-wide

in distribution and known by name to entomologists everywhere. What is written about it by different persons on different continents is immediately intelligible to persons on other continents, and papers published on the biology of members of the genus are easily catalogued and can easily be found by interested persons everywhere. Also, some aspects of the broader zoogeography of these beetles are best understood if generic lines are broad. On the other hand, specialists working on *Cicindela* know that the genus can be divided into natural groups, many of them confined to single continents (see Rivalier, 1950–1963), and recognition of the groups as subgenera helps specialists catalogue the species, indicate phylogenies, and describe local distribution patterns.

For another example, *Chlaenius* (Part III, pp. 20ff) is a huge, world-wide genus of 700 or 800 or more known species. The genus as a whole seems natural (monophyletic), and although it can and should be subdivided, the taxonomic level of the subdivisions should be determined by utility and intelligibility. *Chlaenius* too, like *Cicindela*, is known to many entomologists who are not specialists in Carabidae, and there seems much to lose and little to gain by splitting it into many small genera with new and unfamiliar generic names. Some of the small genera segregated from *Chlaenius* by recent authors have names that even I do not recognize, although I am a specialist in Carabidae! Here again recognition of one genus for general intelligibility, and division into many small subgenera for the utility of specialists, seems the most useful taxonomic treatment.

Those who dislike subgenera may of course use species groups instead.

As to characters which distinguish genera, I know none which, of itself, is always of generic value. I have discussed this fact in detail for the Agonini (Part II, p. 105), and it is true of Carabidae in general. The primary criterion which I have tried to use is actual relationship as shown by a sum of characters. In practice, in cases in which I have been forced to make new generic classifications, I have usually treated as genera groups of species which seem to be closely related among themselves but much less closely related to other species, and which share at least two distinctive characters, one of which may be a distinctive form or appearance. In some cases I have given weight to continuity of variation; that is, I have included in one genus species which are very unlike if the differences between them are bridged by a series of intermediate species. An example of this is discussed in notes under the genus *Nebriagonum* (Part II, pp. 236–237). Fortunately, except in the Agonini (for which see Part II), most New Guinean carabids can be assigned to previously known, often well-known genera. In fact I have been forced to describe only nine new non-agonine genera from New Guinea (cf. [66] and Table 13).

The criteria briefly outlined above fail in some cases, especially among some Agonini that are apparently actively evolving and diversifying in New Guinea now. In these complexly evolving assemblages, in which relationships are obscured by absence of well-defined group characters and by probable occurrence of much parallelism (for example in loss of setae), I have found the most useful treatment is to make "genera of convenience," each containing a number of species which have certain common characters but which may not be directly related among themselves. Three such genera of convenience are used for New Guinean agonines: *Notagonum*, *Colpodes* (in a restricted sense), and *Altagonum* (see Part II, pp. 127ff, 158ff, and 185ff). Of course genera of convenience are temporary, and should be abandoned when the real relationships of the species concerned have been elucidated by third-stage taxonomic work.

[10] *Species.* In contrast to the genus the species does have natural limits, a

least in theory and probably also often in fact. So far as it can be simply defined, a species is a population or group of interbreeding populations which is reproductively isolated from other populations. I cannot here discuss all the practical difficulties and complexities that taxonomists find in applying this definition, but I must mention a few that concern New Guinean Carabidae.

New Guinea is an island. On relatively small islands, for example on some of the West Indies where areas are smaller and where species of Carabidae are fewer than on New Guinea, specific populations on a given island seem to be better defined and easier to distinguish than species of the same genera on continents. The chief difficulty on such islands may be to decide whether slightly different populations on different islands should be considered subspecies or species. Some taxonomists, applying the criterion of reproductive isolation strictly, and assuming that genetic exchange does not occur among the island populations, call every island population a species, no matter how slightly defined it may be. But I think it is more intelligible and more useful to treat slightly differentiated populations on different islands as subspecies, for this seems to me to clarify distribution patterns and relationships.

However, New Guinea is so large, and the species of Carabidae on it are so numerous, that the situation is more like that on a continent than on a small island. Some carabid species apparently are fairly uniform over the whole of New Guinea, but geographic differentiation of many other species occurs in different parts of the island even at low altitudes, and very extensive radiation of species has occurred on New Guinea in some genera [92], especially *Demetrida* (Part III, pp. 140ff). Even in fairly simple cases it is not safe to assume that all New Guinean individuals of a species form one population, which can be compared with and differentiated from (say) all Australian individuals of the same or a related species. An illustration of this point will be found in *Notes* under *Pheropsophus verticalis* (Part III, pp. 236–237).

The difficulty of distinguishing species of Carabidae in New Guinea has been increased by the nature of available material. In spite of the large total number of specimens [2], the representation of many species is still inadequate, and the specimens are sometimes in poor condition. In general, in treating the more complex situations on New Guinea (as on continents), I have followed what I have referred to elsewhere (Part III, p. 146) as a rule of the trade: a taxonomist doing an extensive piece of work must do the best he can with the available material in the available time, and leave details for third-stage taxonomy later.

Although, because of the large size of the island and the large number of species of Carabidae on it, situations on New Guinea as a whole are often complex and difficult to analyze, local situations are more obvious. (This is true on continents too.) At Dobodura, for example, although a number of species of *Notagonum* occurred there (Part II, pp. 127ff), the species were almost all clearly different from each other *at that locality*, and different related species often occupied different habitats. The difficulty has been to decide how slightly-different populations in other parts of New Guinea are related to the Dobodura populations.

In summary, my species are primarily subjective, but my subjective decisions are based not only on comparison of characters visible in museum specimens but also to some extent on occurrence of the insects in the field, and I think they conform reasonably well to reality.

[11] *Subspecies.* The subspecies is now usually defined, in zoology, as a recognizable *geographic* population. I have discussed subspecies in connection with New Guinean Carabidae in Part I, pages 331–

332, and Part II, pages 111–112. They seem to me to be populations which have begun to diverge and which are potentially capable of becoming species, although many or most subspecies probably never do become species. I think it adds to the intelligibility and usefulness of taxonomic work to recognize subspecies, in moderation.

Three kinds of situations occur in New Guinea that can be expressed by trinomials —by use of subspecies. First, a population that is spread over the whole of New Guinea may be slightly differentiated from related populations on other islands. An example is *Chlaenius bimaculatus pongraczi* (Part III, p. 27). Second, a species that is widely distributed on New Guinea may occur in a habitat that is discontinuous on the island. Such a species may be broken into slightly different, geographically isolated subpopulations or subspecies on different mountain tops, or on different river systems, etc. The subspecies of *Lithagonum annulicorne* (Part II, pp. 176–180) illustrate such a pattern of differentiation on different river systems. (However, acquisition of more material from more localities may show this kind of pattern to be too complex for subspecific treatment within the limits of New Guinea.) Finally, a species may be widely and more or less continuously distributed on New Guinea but may vary from locality to locality. Probable examples are found in *Altagonum vallicola* (Part II, pp. 190–191) and *A. grossulum* (Part II, pp. 191–193). (In these cases, too, acquisition of more material is likely to show that, even within the limits of New Guinea, situations are too complex to be reduced to simple systems of subspecies.) I have used subspecies in all the three kinds of situations described and exemplified above. But I have used them sparingly, only when I think they really do clarify situations, or sometimes as a stratagem to emphasize that geographic differentiation occurs even though I am not sure subspecific treatment will be best in the end. I have in fact recognized subspecific differentiation within New Guinea in only 16 of the 667 full species of Carabidae on the island (cf. Table 12 in section [66]).

[12] *Nature of taxonomic characters.* It is a good working taxonomic principle that no characters are inherently of generic, or specific, or subspecific value. Characters used by taxonomists are significant not in themselves but because, in particular cases, they do in fact characterize what seem on the sum of all evidence to be natural and useful genera, or natural species, or useful subspecies. Key characters, including many of the characters used in my keys to New Guinean Carabidae, are therefore primarily tags for the identification of taxa which have other, fundamental but less obvious bases.

For example, the inner wings of Carabidae may be either fully developed or vestigial. Carabid taxonomists (including Sharp, when he wrote the carabid volume of *Fauna Hawaiiensis* about 1900) formerly assumed that atrophy of wings must be a profound evolutionary process and that winged and "wingless" carabids *must* go in separate genera no matter how similar the insects might be otherwise. Now we know that wing atrophy begins by mutation from a long-winged to a short-winged condition, that fully developed and vestigial wings may be inherited in simple Mendelian fashion, and that long- and short-winged individuals of a species often occur together in nature [21]. Under these circumstances the taxonomic significance of state of wings depends on the situation in each case.

In some cases, all known species of what appear (on the sum of other characters) to be natural genera have either fully developed or atrophied wings, and state of wings is then useful in defining and recognizing genera. Among apparently natural genera of New Guinean Agonini (Part II), for example, *Plicagonum, Iridagonum,* and *Maculagonum* (and others)

are always fully winged; *Idiagonum, Nebriagonum,* and *Laevagonum* (and others) are always vestigially winged; and only *Gastragonum* is, as a genus, dimorphically winged. (I have omitted genera of convenience and doubtfully natural genera from these lists.)

In other cases, within what appear to be natural genera, some species are always (so far as known) fully winged while other species always have atrophied wings, and in these cases state of wings is useful in defining and recognizing species. For example, some species of *Gastragonum* (Part II, pp. 222ff) seem always to have fully developed wings, others always atrophied ones (although one species of the genus is known to be dimorphic), and in *Clivina,* although most are fully winged, two New Guinean species (*toxopei,* Part I, p. 36, and *kubor,* see *Taxonomic supplement*) probably always have atrophied wings (but two others are dimorphic). Both long- and short-winged species occur in New Guinea also in the genera *Lesticus, Tachys, Oodes* (of the *terrestris* group), *Scopodes,* and *Pheropsophus* (and dimorphically winged species too occur in all these genera, except perhaps in *Pheropsophus.*)

In still other cases, what appear to be different geographic populations of single species differ in wing state, and in these cases state of wings becomes useful in defining subspecies. Examples among New Guinean Carabidae are *Clivina deälata* (Part I, pp. 372–374) and *Tachys serrula* (Part I, pp. 408–409).

Finally, in a few species in New Guinea (and in many more species in some other parts of the world) long-winged and short-winged individuals occur together, in single populations, and in these cases wing-state has no taxonomic significance. Examples among New Guinean Carabidae include *Clivina crugatella, Tachys avius, Gastragonum terrestre,* and others [21].

These examples show that state of wings of Carabidae has no inherent taxonomic value, but can be used to characterize genera, species, or subspecies in appropriate cases. The same generalization can be made about presence or absence of setae. Certain setae, especially those over the eyes, on the prothoracic margins, and on the third intervals of the elytra, are very useful in carabid taxonomy. However, the setae, like the wings, are often lost apparently by mutation; this is indicated by the fact that some species of Carabidae are dimorphic with respect to setae [100]. So, although presence or absence of particular setae often characterizes genera or species, each case has to be carefully examined to determine what taxonomic value (if any) the setae really have. And when it is found that setae do in fact characterize genera or species, it must be remembered that they are not inherently significant but just happen to be useful taxonomic tags in the cases in question. The effects of mutation and dimorphism on certain taxonomic characters are further discussed in [100].

[13] *Secondary sexual and genitalic characters.* Although as a general principle no taxonomic characters are inherently significant at particular levels, experience shows that certain classes of characters are more likely than others to define broad groups. This is true of characters drawn from secondary sexual structures and from the male genitalia.

Secondary sexual characters, among Carabidae especially the form and clothing of the male front (and often middle) tarsi, are likely to characterize groups of genera. For example, in the tribe Pterostichini a group of genera centering on *Loxandrus* (Part I, pp. 549ff) is characterized partly by having the male front tarsi *obliquely* dilated. In the tribe Harpalini (Part III, pp. 38ff, esp. *Key* on pp. 40–41) the clothing of the male tarsi (whether dense pads or double rows of squamae) helps divide the tribe into what seem to be natural groups. And in many other Carabidae the male tarsal clothing sug-

gests the relationships of difficult genera. However, use of this character is limited by the fact that the tarsal clothing is often lost, the male tarsi being then secondarily simple.

Characters drawn from the male genitalia are more diverse and even more likely to be broadly significant. Their significance varies. The form of the organs as a whole and also the form of the parameres often yield characters of tribal or even subfamilial value. On the other hand, the form of the apex of the middle lobe is likely to yield characters of only specific value, and in some cases the apex varies so much that it can hardly be used in taxonomy at all. Characters drawn from the armament of the internal sac are often intermediate in value; they often define not only single species but also groups of species within genera.

Although genitalic characters are useful and often decisive in carabid taxonomy, and although no group of Carabidae can be considered thoroughly worked out taxonomically until genitalic characters have been utilized or at least considered (they fail in exceptional cases), I have not attempted to use them in my work on New Guinean Carabidae. Genitalic characters (like other characters) do vary, and the extent of variation cannot be predicted. Many specimens throughout the range of each species must be dissected before the amount and distribution of variation can be determined. For example, the apex of the middle lobe is obviously different in selected individuals of *Trichotichnus altus* and *T. dux* (Part III, p. 250, Figs. 172, 173), but proper use of this character to distinguish these and related species would require dissection of several hundred individuals. This kind of study belongs to third-stage taxonomy. I have not time to do it properly. To use genitalic characters improperly, dissecting only a few individuals, too often leads to overemphasis of slight differences and the making of far too many "species" based on characters of no real value.

Although I have for the most part ignored genitalia in my work with New Guinean Carabidae, I have figured them in special cases, especially for the type species of new genera and for a few important new species of which my material is too limited for wide distribution. In these cases genitalic characters are given to aid in placing the genera and species, not to distinguish the species from related ones.

[14] *Preservation of material.* Discussion of genitalic characters leads to consideration of methods of killing and preserving Carabidae. In specimens killed dry, for example in ethyl acetate, the genitalia are not everted and the internal sac is usually fully retracted. The complex patterns of setae and bristles formed by the armament of the sac are then comparable from specimen to specimen. But my New Guinean material was killed and preserved in alcohol, and in alcohol-killed specimens the internal sac is often partly everted but not wholly so, and the spine-and-bristle patterns are confused and cannot be compared from specimen to specimen. This is a very serious disadvantage of alcohol-killed material, and is a secondary reason for my not attempting to use genitalic characters in my work on New Guinean Carabidae.

I should add that I was forced to use alcohol in New Guinea, and that it has positive advantages as well as disadvantages, especially in the tropics. Properly preserved in alcohol, the specimens are safe from mice, insect pests, mold, and rotting. The mouthparts and surfaces are clean and ready for examination with a minimum of trouble after the material is mounted. And killing and preserving in alcohol requires a minimum of time in the field, when time is critical. These advantages of alcohol exist only when alcohol is properly used. It should be grain alcohol of about 70 per cent. Not too many specimens should be put into one vial; the

specimens will be distorted and may rot if packed too closely. And if the alcohol in which the specimens are killed becomes diluted or greasy, it should be poured off and fresh 70 per cent alcohol poured in.

Every good set of instructions for collectors emphasizes that each vial or other unit of specimens should be clearly labeled *immediately* with locality, date, and collector's name. Field numbers should NEVER be used in lieu of this minimum information. Numbers can legitimately be added to the basic data to refer to notebooks with additional information too extensive to put on the field labels.

[15] *Taxonomic methods and procedures.* My work is second-stage faunal taxonomy as described in Part I, pages 328–330. My methods are deliberately designed to allow me to cover the whole carabid fauna of New Guinea at this taxonomic level within a reasonable time. Actually, my study of New Guinean Carabidae has been spread over more than twenty years, although this work has been interrupted for long periods from time to time while I did other things.

My methods of drawing descriptions are described in Part II, pages 92–94; Part I, page 330; and Part III, pages 3–4. The descriptions follow a generally consistent model but are flexible in detail, and I have varied the detailed treatment to fit the importance or interest of each group. I have treated the Cicindelinae (Part I, pp. 330ff) comparatively briefly, because they are outside my usual range of interest, and I have treated the Agonini (Part II) at greatest length because of my special interest in them and because they have radiated most extensively on the mountains of New Guinea. Other tribes have been given something like average treatment. For reasons given elsewhere [6] I have made my descriptions shorter and shorter during the course of my work, because I think that future work should be based on re-examination of specimens more than on descriptions.

For reasons given in Part I, page 4, I have not attempted to see the types of all previously described species of Carabidae that occur in New Guinea. However (under a fellowship of the John Simon Guggenheim Memorial Foundation—see Part II, p. 91), I have been able to study the types and other material in the British Museum, including the H. E. Andrewes Collection, which contains specimens compared with most of the older types of Oriental Carabidae in European museums, and recently (in March, 1968, as part of work done under National Science Foundation Grant GB-93) I have been able to examine also pertinent material in the Muséum National d'Histoire Naturelle in Paris, including types of Dejean and Chaudoir in the Oberthür Collection.

My statements of proportions are based on actual measurements made under a stereoscopic microscope. As I have said before but cannot repeat too often, proportions *cannot* be satisfactorily estimated by eye. The proportions given in my descriptions are usually those of an average-looking male and female, and the specimens actually measured are usually specified in a separate paragraph, *Measured specimens*, although this paragraph is omitted in descriptions based on only one or two individuals. In practice, in making identifications, I keep a slide rule on my desk and calculate proportions on it as I use keys or make comparisons with descriptions.

My statements of total length cover the entire size range of each species. Total lengths have usually been read directly from a millimeter ruler set beside reasonably straight specimens under a stereoscopic microscope. Since length of individuals depends partly on position at death, I think nothing is gained by trying to state it more precisely.

The outline drawings have been carefully prepared as described in Part I, page 4, and are intended primarily to show form, which is very difficult to describe in words.

The eyes, the shape of the prothorax and especially of its posterior angles, the shape of the elytra and especially of their apices, and the positions of supraocular, lateral-pronotal, and dorsal elytral setae or punctures are shown accurately and have been checked by me. Other details are semi-diagrammatic: the mandibles, antennae, legs, for example, are indicated only to show the general appearance and "build" of the insects and are not accurate in detail. A drawing with these characteristics can be made in an hour or two. A drawing of a whole carabid accurate in all details would require at least a day or two of the time of a highly skilled artist, and would require very time-consuming checking by me. So, my outline drawings, like my descriptions, are calculated for present purposes, and have been held within the limits of the time and funds available.

My actual procedure in attacking taxonomic problems is exemplified by the very difficult problem of New Guinean *Demetrida*, as described in Part III, pages 145–146. The method is to alternate between the general and the particular: first to sort individuals into apparent species in a general way and to make a preliminary key, then to draw detailed descriptions of each particular species to determine its characters and variation, then to make an improved key and a tentative classification, then to check characters again species by species, etc. This is what Hennig (1966: 21) calls the "method of reciprocal illumination," and it is the method that taxonomists always have used and always should use. This method leads to continual improvement, never to perfection. Perfection is not attainable in taxonomy.

In selecting new specific and generic names, I have used especially Roland W. Brown's (1956) *Composition of Scientific Words*. I have tried to keep new names short, and (I am not a purist!) I have occasionally shortened them by informal elision, by dropping out one or more syllables of too-long words. I have not thought it necessary to explain the derivation of new names, except in a few cases. Every working taxonomist should have Brown's volume or something like it, and should be able to find the meanings of new names in it. I have also used as specific names the names of appropriate localities, as nouns in apposition.

[16] *Data sheets*. As a basis for summarizing and analyzing the New Guinean carabid fauna, I have prepared a set of 30 data sheets (Fig. 6) on which are listed all the Carabidae proper (excluding Cicindelinae) now known from New Guinea. Sets of these sheets will be deposited at the British Museum, the Bishop Museum in Honolulu, and CSIRO in Canberra, Australia.

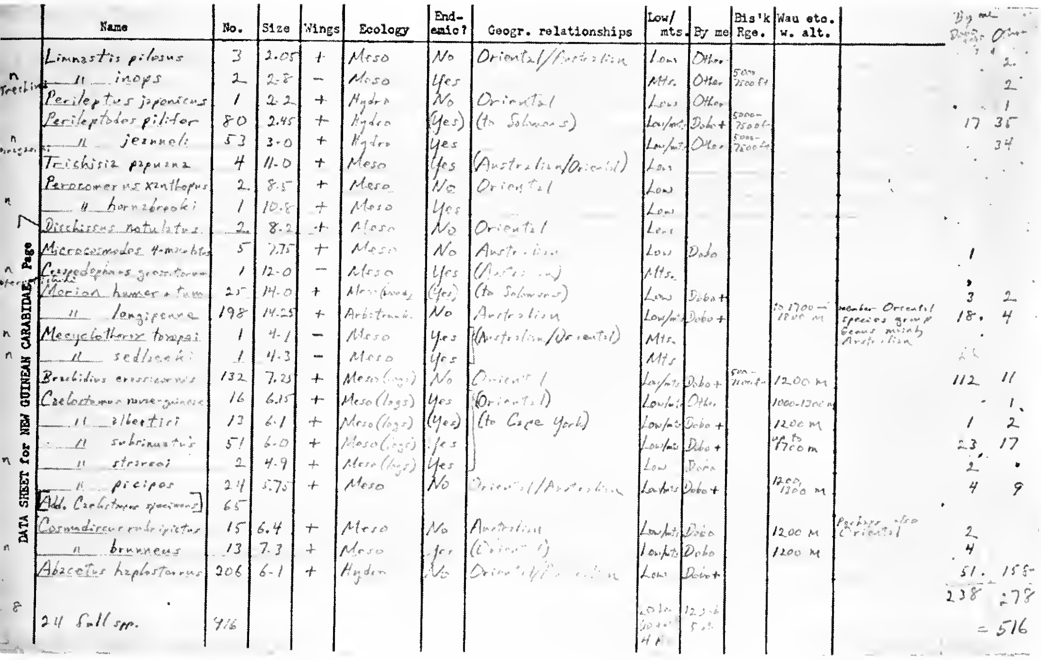
On these sheets, the first regular column lists the names of all New Guinean Carabidae treated in Parts I-IV, arranged in taxonomic order, with species recorded or described in the *Taxonomic supplement* of Part IV inserted in their proper positions. The "n's" in the left-hand margins of the sheets indicate which species are described as new.

The second column ("No.") gives the total number of specimens of each species or subspecies actually recorded from New Guinea in Parts I–IV.

The third column gives the mean size of each species to the nearest 0.05 mm.

The next column ("Wings") indicates, by signs described in the text [21], whether the wings are fully developed, reduced, or dimorphic.

The column "Ecology" indicates the gross habitat of the *lowland* species, so far as habitats are known or can reasonably be deduced. "Meso" indicates found on the ground not associated with surface water; "Hydro," associated with surface water (streams, or swamps, or other wet places); "Arb," arboreal. Additional words in some cases indicate habitat more precisely: whether arb(oreal) species occur on trunks or in foliage, which meso(philes) occur chiefly in wood debris or (rotting)



DATA SHEET for NEW GUINEAN CARABIDAE Page 7

Name	No.	Size	Wings	Ecology	Endemic?	Geogr. relationships	Low/mts.	By me	Bis'k Rge.	Wau etc. w. alt.		By me	Other
Limnastis pilosus	3	2.05	+	Meso	No	Oriental/Australian	Low	Other					2
" inops	2	2.8	−	Meso	Yes		Mts.	Other	5000–7500 ft				2
Perileptus japonicus	1	2.2	+	Hydro	No	Oriental	Low	Other					1
Perileptodes pilifer	80	2.45	+	Hydro	(Yes)	(to Solomons)	Low/mts.	Dobo +	5000–7500 ft			17	35
" jeanneli	53	3.0	+	Hydro	Yes		Low/mts.	Other	5000–7500 ft				34
Trichisia papuana	4	11.0	+	Meso	Yes	(Australian/Oriental)	Low						
Peronomerus xanthopus	2	8.5	+	Meso	No	Oriental	Low						
" hornabrooki	1	10.8	+	Meso	Yes		Low						
Dischissus notulatus	2	8.2	+	Meso	No	Oriental	Low						
Microcosmodes 4-maculatus	5	7.75	+	Meso	No	Australian	Low	Dobo				1	
Craspedophorus grossitorum	1	12.0	−	Meso	Yes	(Australian)	Mts.						
Morion humeratum	25	14.0	+	Meso (wood)	(Yes)	(to Solomons)	Low	Dobo +				3	2
" longipenne	198	14.25	+	Arb: trunk	No	Australian	Low/mts.	Dobo +		to 1700–1800 m	member Oriental species group Genus mainly Australian	18	4
Mecyclothorax toxopei	1	4.1	−	Meso	Yes	(Australian/Oriental)	Mts.						
" sedlaceki	1	4.3	−	Meso	Yes		Mts						
Brachidius crassicornis	132	7.25	+	Meso (logs)	No	Oriental	Low/mts.	Dobo +	5000–7000 ft	1200 m		112	11
Coelostomus novaeguineae	16	6.15	+	Meso (logs)	Yes	(Oriental)	Low/mts.	Other		1000–1200 m			1
" albertisi	13	6.1	+	Meso (logs)	(Yes)	(to Cape York)	Low/mts.	Dobo +		1200 m		1	2
" subsinuatus	51	6.0	+	Meso (logs)	Yes		Low/mts.	Dobo +		up to 1700 m		23	17
" straneoi	2	4.9	+	Meso (logs)	Yes		Low	Dobo				2	
" picipes	24	5.75	+	Meso	No	Oriental/Australian	Low/mts.	Dobo +		1200, 1300 m		4	9
[Add. Coelostomus specimens]	65												
Cosmodiscus rubripictus	15	6.4	+	Meso	No	Australian	Low/mts.	Dobo		1200 m	Perhaps also Oriental	2	
" brunneus	13	7.3	+	Meso	Yes	(Oriental)	Low/mts.	Dobo		1200 m		4	
Abacetus haplosternus	206	6.1	+	Hydro	No	Oriental/Australian	Low	Dobo +				51	155
												238	278
24 full spp.	416						[illegible]	[illegible]					= 516

Figure 6. One of 30 data sheets on which details of New Guinean Carabidae have been tabulated. See text for further explanation.

logs, etc. These indications of habitat are based primarily on my own observations. However, my field notes are scanty; some species that I collected were not recognized in the field; and the habitats of some other species are simply assumed to be the same as the habitats of their closest relatives (but see [25]). There are therefore probably some errors in the "Ecology" column, although the ecologic composition of the New Guinean carabid fauna as a whole, based on this information, is surely approximately correct.

The next column ("Endemic?") indicates, by "Yes" or "No," whether or not the species are endemic to (=confined to) New Guinea. In the case of species which occur mainly in New Guinea but which extend to certain not-too-distant islands, the "Yes" in the "Endemic" column is placed in parentheses, and occurrence outside New Guinea is indicated in the next column.

The column headed "Geogr(aphic) relationships" indicates the principal occurrence outside New Guinea, or the closest geographic relationships of each species of which the relationships can be determined. "Oriental," for this purpose, is taken to include the Philippines and Celebes, and "Australian" indicates occurrence in Australia *beyond Cape York*. These words without parentheses indicate that the New Guinean species themselves occur in the Oriental area or Australia. The same words in parentheses indicate that the apparent closest relatives of the New Guinean species occur in the areas indicated. Also in this column are indicated slight range extensions of New Guinean species to New Britain, or to the Solomons, or to the Cape York peninsula but not farther into Australia.

The next column ("Low/mts.") indicates altitudinal occurrence. "Low" means recorded below 500 m (1640 ft.); "Mts.," recorded above 1000 m (3280 ft.); and

"Low/mts.," recorded both below 500 m and above 1000 m. "Int." is used for species thus far reported only between 500 and 1000 m, and not assignable to either the lowland or the mountain faunas. A few species, known only from old specimens, are from unknown altitudes.

The next column ("By me") indicates species that I collected, those found at Dobodura being indicated by "Dobo," and those that I took only at other localities, by "Other."

The next column indicates species taken, chiefly by myself, on the Bismarck Range, with altitudes indicated; and the next, species found at or in the vicinity of Wau, again with altitudes indicated.

The last regular column is used for special notes: if the New Guinean population is an endemic subspecies of a more widely distributed species; if a species widely distributed outside New Guinea reaches only the western, southern, or eastern part of the island; if a species that is winged on New Guinea is dimorphic elsewhere; etc. And the wide right-hand margin of the sheets is used for various calculations, especially for reckoning the number of specimens taken by myself at Dobodura and elsewhere—the extent of my own collecting is of some interest as indicating the extent of my knowledge of habitats.

For some columns, but not all, totals have been calculated and are entered at the bottom of the sheets, and the sheet totals are added on a separate page labeled "Data summary of New Guinean Carabidae."

ANALYSIS AND DISCUSSION

[17] *New Guinea.* New Guinea is a huge island, the largest fully habitable island in the world, stretching about 1500 miles (2400 km) from the tip of the Vogelkop to Milne Bay, with an area of roughly 300,000 square miles (nearly 800,000 sq. km). The position of New Guinea in relation to other land areas is shown in the map in Figure 1. This map shows also, by broken lines, the extent of the continental shelves of Asia and Australia.

The whole backbone of New Guinea is mountainous, with many ranges rising from 12,000 to over 14,000 feet (3660 to 4270 m), the highest point being over 16,000 feet (over 4880 m) in the Snow Mountains of West New Guinea. The island includes extensive lowlands too, with several enormous river deltas.

New Guinea is tropical, and the most obvious and most widely spread vegetation is tropical rain forest. However, extensive opener woodlands, grasslands, and swamp forests occur also at low altitudes, and altitudinal vegetations are stratified on the mountain slopes, with bare rock at still higher altitudes and permanent snow on a few of the highest summits in West New Guinea. More details are given under *Ecology: habitats* [24].

As to history, the geologic evolution of New Guinea is surprisingly little known. Umbgrove (1949) indicates the complexity of the history of the whole Indo-Australian Archipelago. David (1950, Vol. 1, p. 681) says that the physiography of New Guinea and adjacent islands "reflects the dominating influence of young and intense orogenic processes." And Browne (1958, in *The Australian Encyclopaedia*, Vol. 6, pp. 452–453) summarizes chronologically what is known of the geologic history of the eastern half of the island. From these sources we may conclude, probably correctly, that the history of New Guinea has been complex, that parts of the island may be old, but that many features including the principal mountain ranges are geologically recent. New information and a new synthesis of what is actually known about the geology and geologic history of the whole island are very much needed.

As to geographic history, when sea level fell at times in the Pleistocene, the continental shelves outlined in Figure 1 were mostly or wholly land. New Guinea was then surely connected to the continent of

Australia; the last such connection ended only about 10,000 years ago. At the same times water gaps toward Asia were narrower than now. The situation before the Pleistocene is not clear: connections with Australia are likely, but a complete land connection with Asia can hardly have existed in the Tertiary (that is, during the age of mammals), and even a pre-Tertiary connection with Asia is doubtful. This is said of New Guinea as a whole. Of the mountains it can be said more specifically that there seems to be no geologic evidence that mountain ranges on New Guinea have ever been connected with ranges on any other land, and this evidence is consistent with that of the mountain carabid fauna of New Guinea, which has little relationship with montane faunas elsewhere, and most of which has apparently evolved *in situ* from lowland ancestors [90].

Finally, the biotic history of New Guinea has evidently been complex. The island has been on the dispersal routes of many plants and animals moving, one way or the other, between Asia and more-southern lands (New Caledonia and New Zealand as well as Australia). Present relationships are complex. For example, northern-related oaks and southern-related *Nothofagus* ("southern beeches") occur together in the mountains of New Guinea. And it is likely that many groups of plants and animals that dispersed across the island in the past have disappeared there. The fossil record on New Guinea is too scanty to reveal many details, but indirect evidence allows us to make hypotheses about the origin and evolution of parts of the New Guinean fauna, including the Carabidae (see items under *Zoogeography* and *Evolution* in *Contents*).

The history of man in New Guinea is briefly traced by Biskup et al. (1968). Although prehistoric men may have reached New Guinea as much as 50,000 years ago, and although Europeans began to explore the coast of the island more than 400 years ago, man has (I think) had only a moderate impact on the plant cover and native fauna. Some areas of grassland have been increased at the expense of forest by clearing and burning for primitive agriculture and, later, for the establishment of coconut plantations, but enormous stretches of rain forest still remain. Hunting for food by primitive man has presumably reduced populations of some mammals, birds, and reptiles, and may have caused extinction of a few species in New Guinea. For example, the Tasmanian Wolf, which is now confined to the island of Tasmania (if it is not extinct even there), has been found subfossil at a prehistoric camp site in New Guinea. And introduction of pigs, which run wild and have modified large areas of the rain-forest floor by their rooting, has probably affected the distribution of some ground-living invertebrates. But I think the sum of all these factors on Carabidae in New Guinea has probably not been great. The most important effect may have been to facilitate dispersal of some common species that live in grassland, including some primarily lowland species that have apparently invaded mid-altitudes in places after the clearing of forest [26].

Further information about the eastern half of New Guinea can be obtained from *The Australian Encyclopaedia* (1958; under "Papua and New Guinea") and from a compact, well-illustrated small book by Lea and Irwin (1967).

[18] *The New Guinean carabid fauna: taxonomic composition.* The *Coleopterorum Catalogus* (Csiki, 1927–1933), covering the world as a whole, recognizes 70 tribes of Carabidae (exclusive of Cicindelinae), or 71 if the Agonini (considered a subtribe of Pterostichini by Csiki) are given tribal rank, and the number is increased to 72 if the Paussini (placed in a separate family by Csiki) are added. Of these 72 tribes, 25, or about one third, are represented in New Guinea. These tribes are listed, and the number of New Guinean

TABLE 1. TRIBES OF CARABIDAE PROPER REPRESENTED IN NEW GUINEA, WITH NUMBERS OF NEW GUINEAN SPECIES

Tribe	No. of species in New Guinea
Ozaenini	1
Paussini	1
Scaritini	30
Bembidiini	72
Trechini	3
Panagaeini	6
Pterostichini	46
Agonini	160
Perigonini	14
Licinini	8
Chlaeniini	12
Oodini	13
Harpalini	53
Anaulacini	4
Cyclosomini	1
Lebiini	160
Pentagonicini	15
Hexagoniini	2
Odacanthini	18
Dryptini	5
Zuphiini	8
Helluodini	10
Helluonini	10
Brachinini	7
Pseudomorphini	8
	667

species in each indicated, in Table 1. Some changes in tribal classification have been made since publication of the *Catalogus*, and some authors have greatly increased the number of tribes by splitting ("taxonomic inflation"), but the splitting has not increased the proportion of tribes represented in New Guinea, and the *Catalogus* is still the most convenient basis for arranging the data that I want to present. These tribes are individually discussed in the following pages under item numbers [33–57].

Of these 25 tribes represented in New Guinea, the Scaritini include most of the fossorial species. The Bembidiini include most of the very small species, especially on the ground (some small arboreal species are lebiines). The Pterostichini are notable for representing perhaps a relatively old fraction of the fauna (but apparently no New Guinean Carabidae are very old), and for including several endemic genera at high altitudes. The Agonini are dominant on the ground (but a few are arboreal) and especially at higher altitudes. The Harpalini are dominant on the ground in grassland and in other relatively open places (but some occur in rain forest too). And the Lebiini are dominant in arboreal habitats (although some are ground-living), especially in rain forest. This is, I think, a sufficient introduction to the taxonomic composition of the New Guinean carabid fauna as a whole.

[19] *Numbers of species.* The number of full species of Carabidae proper (exclusive of Cicindelinae) now known from New Guinea is 667. These species are tabulated on the data sheets described above [16].

The lowland and mountain-living carabid faunas of New Guinea can usefully be distinguished and compared. I have arbitrarily considered as lowland species all those actually recorded below 500 m (*c.* 1640 ft.), and as mountain-living all those recorded above 1000 m (*c.* 3280 ft.). Many species that occur below 500 occur also above 1000 m: 161 such species are now known, and the number will probably be much increased in the future. Some of these species are common over a wide range of altitudes. Others are primarily lowland forms which occasionally occur above 1000 m in suitable habitats. And others are primarily mountain-living forms which descend below 500 m in suitable habitats. (See discussion of altitudinal range in relation to habitat under *Altitude* [26].) A few (18) species that have thus far been found only between 500 and 1000 m, or at localities of which the altitudes are doubtful, cannot now be assigned to either lowland or mountain faunas.

Of the total of 667 full species of Carabidae now known from New Guinea, 434 have been found in the lowlands, below 500 m altitude. My impression is, judging from the small number of additional spe-

cies that turn up in new collections, that relatively few primarily lowland species remain to be discovered, although many primarily mountain-living species will probably be found to occur below 500 m in places.

The number of species at a single lowland locality in New Guinea may be more significant than the total number of lowland species on the island. At Dobodura, Papua, I found 217 species in about four months of collecting. Dobodura is a strictly lowland locality; my collecting was done under difficulty; and my collection from there is surely incomplete, being especially deficient in arboreal species. (See Part I, pp. 325–326, and the present part [3, 5] for further description of this locality and of my collecting there.) I think that a year's unhampered collecting by a competent carabid specialist would surely raise the number of species at Dobodura to more than 250, and perhaps to more than 300. Although a few species are still known only from Dobodura, the majority found there are widely distributed over much or all of New Guinea.

Because the Carabidae of most other islands in the Indo-Australian Archipelago, excepting Java (see [64] and Fig. 13), are not well known, I have to go to the other side of the world for comparative data. The Carabidae of the Greater Antilles, the four large islands of the West Indies, are well known (better known than those of New Guinea), and I have tabulated numbers of species in relation to areas of the islands in a paper on Carabidae of mountains and islands (1943: 42, Table 1). Inspection of this table yields a rule of thumb: among these islands, if one island is ten times as large as another, the larger island will have about twice as many species of Carabidae.

Of the Greater Antilles, Hispaniola (called also Haiti or Santo Domingo) is most nearly comparable to New Guinea, being ecologically diverse and having extensive mountains. New Guinea (roughly 800,000 sq. km or 300,000 sq. mi. in area) is about ten times as large as Hispaniola (roughly 80,000 sq. km or 30,000 sq. mi.). Hispaniola has a known carabid fauna of 148 species, of which 97 are lowland forms. By my rule of thumb, New Guinea should have a total of about 300 species, of which about 200 should be lowland forms. But figures given in preceding paragraphs show that New Guinea has in fact more than twice as many species as expected by this rule.

The greater richness of the New Guinean fauna may be due partly to the greater ecologic richness and diversity of the island. New Guinea has very large areas of fine rain forest, several big rivers, extensive swamps, etc., while the Greater Antilles have relatively little, relatively poor rain forest, no really large rivers, and few large swamps. The greater richness of New Guinea may be due in part also to the greater accessibility of the island, which was connected by land to Australia at times in the Pleistocene, and which many Carabidae have reached from the west too.

The New Guinean carabid fauna is in fact continental in size and diversity. Satisfactory figures for numbers of species in continental areas of Asia and Australia are not available, so again I have to go to the other side of the world for comparisons. In 1943 (p. 41) I counted or estimated numbers of species of Carabidae in several areas in eastern North America including New Jersey, Indiana, and North Carolina. Each of these states has more than 300 but less than 400 species of lowland Carabidae. Most of the species are widely distributed and are shared by all three states, so that the total number of lowland species in all three states together does not much exceed 400. This is considered a rich continental carabid fauna. However, the lowland fauna of New Guinea is evidently still richer—it must be remembered that even the lowland Carabidae of New

Guinea are still much less well known than those of eastern North America.

In 1943 (p. 41) I thought I detected a diminution of numbers of Carabidae from temperate North America into the American tropics, although exact figures were not available. New Guinea can now be seen to have a carabid fauna rich out of all expectation for a lowland tropical area. Evidently Carabidae are very numerous in species in the lowland tropics at least in some regions. (But in proportion to the total insect fauna, Carabidae may still be less numerous in the tropics than in temperate areas.) However, they are evidently much more difficult to find in the tropics than in the north temperate zone, probably because they are more diverse ecologically in the tropics, and perhaps because the tropical populations tend to be sparser. (For further discussion of numbers of Carabidae in the tropics including New Guinea, and of the possible effect of competition with ants, see the present paper [27] and Fig. 11.)

Mountain-living Carabidae, known above 1000 m (*c.* 3280 ft.) in New Guinea, now total 376 full species, of which 161 are and 215 are not known below 500 m. However, this is probably a small fraction of the total number of Carabidae existing on mountains in New Guinea. Until good collections have been made not only on different mountain ranges but also on successive peaks along single ranges, we have no basis for estimating the amount of geographic replacement of localized species that occurs from point to point in the mountains of New Guinea, and no basis for making a real estimate of total number. I can therefore only guess, from the fragmentary collections available, that the total number of mountain-living species of Carabidae in New Guinea will run to many hundreds, perhaps thousands, of species.

The number of species of Carabidae occurring at a single locality at middle altitudes in New Guinea is surprisingly large. For example, 170 species have been taken between 1000 and 2000 m at and near Wau [5], in the Morobe District of North-east New Guinea. (Thirty-five additional species have been found in the same general area either below 1000 or above 2000 m.) The collections at Wau were made by persons (the Sedlaceks and others) who, although fine collectors, are not carabid specialists. Their collections are surely deficient in small ground-living species, although strong in arboreal ones and in light-trap material. The total number of Carabidae existing at and near Wau between 1000 and 2000 m is probably really considerably more than 200 species. Many of the species that occur at Wau occur also in the lowlands, but many others are either confined to the mountains or at least have not yet been found at lower altitudes; some are wide-ranging in New Guinea, others apparently confined to the general vicinity of Wau.

At still higher altitudes in the mountains of New Guinea so little carabid collecting has been done that counts of species are hardly significant. However, the number of species at single localities obviously decreases very sharply with increase of altitude. Incomplete samples (Table 2) show the Snow Mountains in West New Guinea with nine species above 3000 m, including only one above 4000 m, and Mt. Wilhelm in North-east New Guinea with seven species above 3000, including two above 4000 m.

In summary of numbers of species: New Guinea has an unexpectedly large and diverse carabid fauna, large even by continental standards. Of the total number of 667 species of Carabidae proper now known from the island, 434 have been found below 500 m altitude, and many of these are widely distributed on the island. At mid-altitudes (1000–2000 m) species are still numerous; some of them are widely distributed, others localized. At still higher altitudes, numbers of species at single localities decrease sharply, but most of the high-altitude species are localized, and

Table 2. New Guinean Carabidae found above 3000 m (above *c.* 10,000 ft.)

Table gives names, mean lengths, and altitudes of all Carabidae thus far recorded above 3000 m (above *c.* 10,000 ft.) in New Guinea. All species are (probably) ground-living mesophiles except *Nebriagonum percephalum*, which is found beside mountain torrents, and *Maculagonum altipox*, which apparently lives in tussock grass. All species listed are flightless, with atrophied wings, except *Maculagonum altipox*, which has full wings.

Snow Mts., West N. G. (9 species)
Mecyclothorax toxopei (4.7 mm), 4200 m
Rhytiferonia nigra (19.75 mm), to 3300 m
Analoma fortis (12.85 mm), to 3850 m
Analoma gracilis (14 mm), 3800 m
Gastragonum laevisculptum (8.3 mm), 3600 m
Montagonum toxopeanum (9.0 mm), 3600 m
Nebriagonum subcephalum (9.9 mm), 3300 m
Chydaeus papua (9.9 mm), 3600 m
Scopodes altus (3.4 mm), to 3800 m
Mt. Wilhelm, N-E N.G. (7 species)
Mecyclothorax sedlaceki (4.3 mm), 4250 m
Maculagonum altipox (7.0 mm), above 3000 m (winged, in tussock grass)
Nebriagonum cephalum (8.55 mm), to 4250 m (2 collections)
Nebriagonum percephalum (9.9 mm), to above 3000 m (beside running water)
Nebriagonum transitum (9.35 mm), to 3400–3500 m (2 collectors)
Laevagonum subcistelum (5.95 mm), above 3000 m
Chydaeus papua (9.9 mm), to 3400–3500 m (several collectors)
Mt. Albert-Edward, Papua (3 species)
Analoma rosenburgi (12.6 mm), 4026 m
Montagonum filiolum (10.5 mm), 3660 m
Fortagonum antecessor (9.0 mm), 3660 m
Mt. Giluwe, Papua (1 species)
Laevagonum giluwe (7.0 mm), 3750 m
Mt. Amangwiwa, N-E. N. G. (1 species)
Montagonum fugitum (11 mm), 3355 m

much geographic replacement occurs, so that the total number of high-altitude Carabidae on the mountains of New Guinea is surely very great, although the final number can not yet even be guessed at closely. This situation is diagrammed in Figure 7.

[20] *Size of individuals.* New Guinean Carabidae are small. Of 434 lowland species (exclusive of Cicindelinae), 388, or 89 per cent, have a mean length of 12 mm (*c.* ½ inch) or less, and only five species exceed a mean length of 20 mm. Of these five, three are characteristic, endemic New Guinean species: *Lesticus politus* (24 mm), *Colpodes rex* (21 mm), and *Chlaenius pan* (25 mm). The other two, still larger species are marginal or introduced: *Gigadema maxillare* (32 mm) is an Australian species of which a single specimen has been found on the southern edge of New Guinea, and *Catadromus tenebroides* (mean 51 mm) is an Australian species of which two specimens were taken at military ports in New Guinea during the war (and which has been found in Java too). So, *characteristic* lowland Carabidae of New Guinea are all small, none more than an inch long, and most much less than that. Mountain-living Carabidae in New Guinea are small, too, none having a mean length of more than 22 mm (less than 1 inch). However, minute species (mean length less than 3 mm), although numerous in the lowlands, become relatively fewer with increasing altitude and disappear at highest altitudes. The few Carabidae known above 3000 m (Table 2) range from 3.4 to 19.75 mm mean length.

Small size is a characteristic of the Carabidae of some other East Indian islands including Celebes and the Philippines. (Sumatra, Java, and Borneo have a few larger Carabidae, notably species of *Mormolyce.*) *West* Indian Carabidae are all small, too.[1] On Cuba, no carabid has a mean length of more than 25 mm (1 inch), and only four (2 species of *Calosoma*, a *Scarites*, and a *Chlaenius,*) exceed a mean of 20 mm; and on Hispaniola only the two *Calosoma* and possibly a *Scarites* exceed a mean of 20 mm. However, the situation is

[1] Since this was written, a very large, large-headed *Scarites* has been discovered in the mountains of eastern Puerto Rico (Hlavac, 1969). The first specimen found measured about 35 mm. It far exceeds in size any of the approximately 350 species of Carabidae previously known from the West Indies.

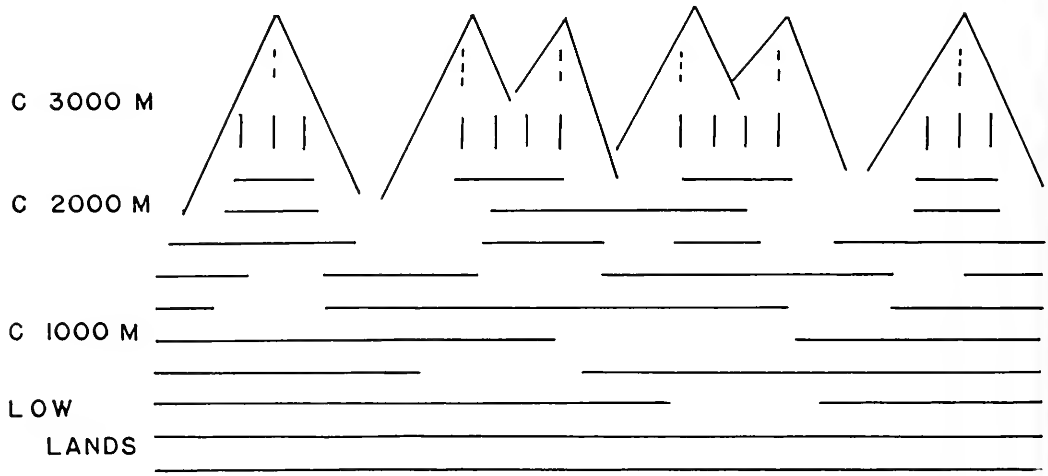


Figure 7. Diagram of distribution of species in relation to altitude among New Guinean Carabidae. The diagram is not exactly quantitative, but each horizontal line, whether broken or not, represents c. 50 species; each unbroken vertical line, c. 10 species; and each broken vertical line, less than 10 species. Unbroken horizontal lines represent species that extend over c. the whole length of New Guinea; broken horizontal lines, species that are more localized. The diagram emphasizes that increase in altitude is accompanied both by decrease in number of species at single localities and by increasing localization of species.

strikingly different on Madagascar. The Carabidae of Madagascar include many very large forms especially in the tribes Scaritini and Pterostichini, some of the Madagascan scaritines being among the largest Carabidae in the world.

The small size of New Guinean Carabidae is not easy to explain. Mere existence on a large island does not necessarily favor smallness: witness the gigantic carabids on Madagascar. Nor does existence in rain forest necessarily favor smallness: witness *Mecynognathus* and the large *Trichosternus* in tropical rain forest in Australia (following paragraph).

Comparison of New Guinean species with the same or related species in Australia and southern Asia indicates no general decrease of size on New Guinea [93]. New Guinean Carabidae are small because small rather than large Carabidae have reached and established themselves on the island. This suggests that difficulty of access has barred large forms, but this explanation is too simple or at least incomplete. New Guinea was connected to Australia at times in the Pleistocene. Many Australian Carabidae including many Scaritini and Pterostichini are large: one of the largest and finest Carabidae in the world, *Mecynognathus dameli* Macleay (mean length *c.* 50, maximum length 63 mm), is confined to a small area of poor rain forest on the tip of Cape York, just opposite New Guinea; other large Pterostichini, especially species of *Trichosternus* (Darlington, 1961), occur in the tropical rain forests at the base of the Cape York Peninsula; and large Carabidae occur in the drier parts of Australia too. Why did not large forms invade New Guinea when there was a land connection in the Pleistocene? Ecologic barriers evidently existed between Australia and New Guinea even when land was continuous [84], but why were the barriers so effective against large carabids living in both rain forest and dry country?

Predation, by mammals and birds, does not explain the absence of large Carabidae in New Guinea. Insectivorous predators do occur there, but they occur also in Australia and Madagascar, where large

Carabidae are common. And on the West Indies, where mammalian predators at least are relatively few, large Carabidae do *not* occur.

In spite of what has been said in the several preceding paragraphs, and although the situation is evidently complex, I think the small size of New Guinean Carabidae may be a result of a combination of three factors: (1) difficulty of access, (2) the greater dispersibility of small as compared with large Carabidae, and (3) time. New Guinea *has* been somewhat isolated, on the west by water barriers which have probably been narrower than now at times in the past but which have existed for a very long time, and from Australia by fairly effective ecologic barriers even when what is now the island was connected with the mainland. Small insects do disperse through the air more readily than large ones; the ancestors of New Guinean Carabidae were not only all small (or at least not very large) but almost all of them were or may have been winged when they reached the island [23, 88]. The small, winged ancestors of New Guinean Carabidae may have crossed barriers which large Carabidae and flightless ones did not cross. This explanation does perhaps account well enough for the initial small size of New Guinean Carabidae. To account for the present smaller size of Carabidae on New Guinea as compared with Madagascar, time must be invoked, I think. The New Guinean fauna is evidently relatively recent in its origins; the Madagascan fauna, probably much older. Also, Madagascar is much more effectively isolated than New Guinea; invasions and replacements probably occur less often; and old stocks probably survive longer and have more time to increase in size. (See [89] for discussion of relative age and rate of turnover of the New Guinean fauna.) So, while the small size of New Guinean Carabidae is not due to decrease of size, the large size of many Madagascan forms may be due to increase of size, the increase having required a relatively long time and relatively effective isolation.

The size distribution of New Guinean Carabidae is, unexpectedly, bimodal. A histogram (Fig. 8) of the distribution by size of all 434 *lowland* species shows not only that most are small but also that separate modes occur at 2.0–2.95 and at 6.0–6.95 mm, with a deficiency especially at 4.0–4.95 mm. A highly speculative and oversimplified explanation can be derived from the possible relation of Carabidae with ants. Very small Carabidae may be able to hide from ants, and relatively large ones may be able to protect themselves, while Carabidae in the 4.0–4.95 mm size class may be especially vulnerable to competition with or predation by ants. If so, this is only one aspect of a probably complex impact of ants on Carabidae and carabid faunas which is further discussed under *Ants* [27].

A simpler explanation of the bimodal size distribution of lowland Carabidae in New Guinea can be derived from the predominance of the single genus *Tachys* (taking the genus in a broad, old-fashioned sense). This is a huge genus of small Carabidae. Although it is well represented in some temperate areas, it is primarily tropical, and includes great numbers of species in the tropics of all continents. Most of the really small Carabidae in New Guinea belong to this genus: the portion of the bimodal histogram (Fig. 8) represented by *Tachys* is shown by hatching in the first three columns of the histogram. Without *Tachys*, the lowland Carabidae of New Guinea have a regular size distribution, with a single mode at or near 6–6.95 mm. The bimodality of the fauna is therefore apparently due to the addition of a large number of species of the predominant genus *Tachys* to what would otherwise be a simpler, unimodal size distribution. But this explanation does not necessarily preclude the preceding one. The small size of individual *Tachys*

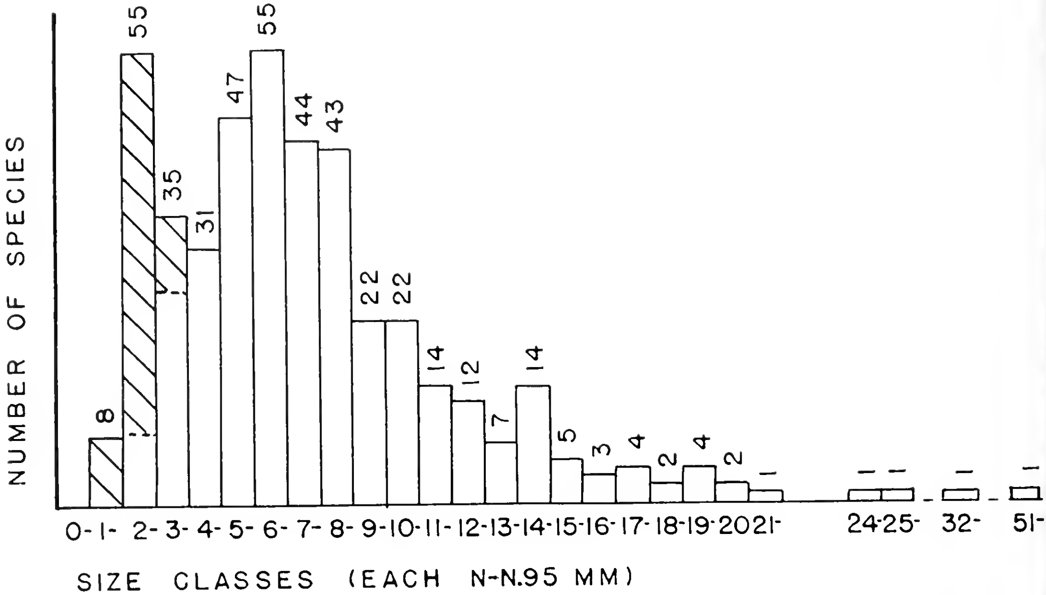


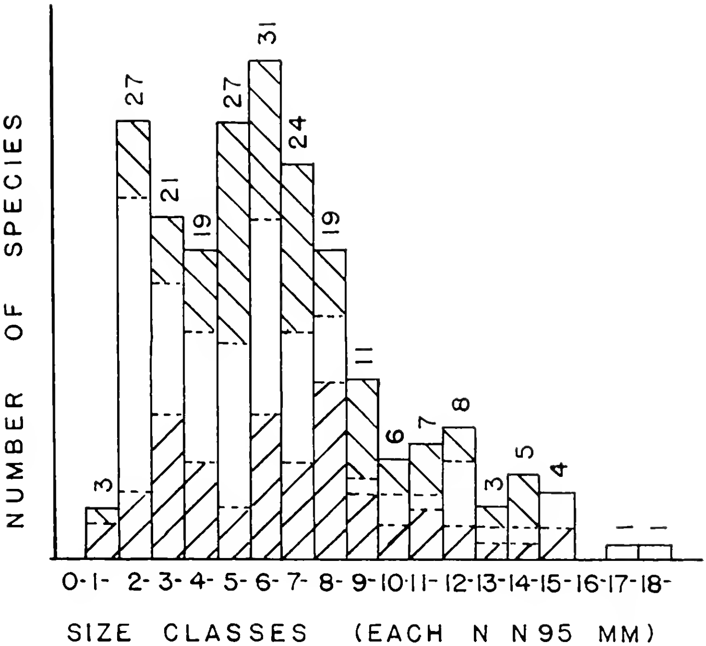
Figure 8. Histogram of size distribution of *lowland* Carabidae in New Guinea. Each species is counted once, according to its median length. Each column represents number of species of which the mean length falls between N-N.95 mm; the actual numbers of species are given above the columns. The hatched portions of the first three columns represent *Tachys*. See text for further explanation.

may be one reason for their great success, and may enable them to live in the presence of dominant ants more successfully than slightly larger Carabidae can do. Although several groups of *Tachys* have certainly radiated to some extent in New Guinea, the number of species there is not due primarily to radiation but to the large number of separate stocks that have reached the island: my data sheets indicate at least 23 separate relationships between different New Guinean *Tachys* and those of other areas, and this suggests at least 23 separate invasions of New Guinea by members of this one genus.

In an attempt to get a more detailed explanation of the two size modes of lowland New Guinean Carabidae, I have made a size histogram (Fig. 9), of the 217 species that I found at Dobodura, indicating the ecologic composition of the size classes. I have limited this diagram to species that I myself collected at one locality, because I know something of their ecology. (See *Ecology: habitats* [24] for further discussion of habitats of New Guinean Carabidae.) This histogram suggests that lowland mesophile Carabidae do have a bimodal size distribution in New Guinea. Mesophiles compete more directly with ants than hydrophiles and arboreal Carabidae do, and would be more likely to show the effects of competition.

My tentative conclusion is that the double-moded size distribution of lowland Carabidae in New Guinea is due to the presence of excessive numbers of small species of *Tachys*, but that this explanation still allows the possibility of an underlying effect of competition with or predation by ants.

Mountain-living Carabidae in New Guinea have a different size distribution from the lowland forms. Figure 10 is a histogram of the sizes of the 215 known strictly mountain-living species. This figure



igure 9. Histogram of size distribution of Carabidae found at Dobadura. Explanation as for Fig. 8, except hatched portions f columns represent ecologic groups: right-oblique hatching at bases of columns, hydrophiles; no hatching, mesophiles; nd left-oblique hatching at top of columns, arboreal forms.

hows a single mode at a larger size—at r near 9–9.95 mm—than the second mode f the lowland species. Very few *Tachys* ccur in the mountains; their place in the istogram is represented by the hatched art of the first column; and removal f *Tachys* from this histogram does not hange it significantly. However, ants too re relatively few at higher altitudes in New Guinea, and their fewness may have omething to do with the size distribution f mountain-living Carabidae.

In summary of the size of New Guinean Carabidae: all the characteristic ones are mall. The absence of large forms may e due to a combination of (1) difficulty f access, (2) the greater dispersibility of mall as compared with large Carabidae, nd (3) the fact that the existing New Guinean carabid fauna is relatively recent n its origins and has not had time to volve large forms. The lowland Carabidae of New Guinea have a bimodal size distribution, with modes at 2–2.95 and 6–6.95 mm; this bimodality is due primarily to the presence of many small species of *Tachys*, but may also reflect an underlying relation with ants, which may compete with or prey on Carabidae especially in the 3 to 5 mm size classes. Mountain-living New Guinean Carabidae have a unimodal size distribution, with the mode at or near 9–9.05 mm; both *Tachys* and ants are relatively few in the mountains, and their absence may partly account for the different size distribution of mountain-living as compared with lowland Carabidae.

[21] *Wings and wing atrophy.* I have a long-standing interest in the wings, wing atrophy, and flight of Carabidae (Darlington, 1936; 1943), and I have been constantly on the lookout for cases of wing reduction among the New Guinean species. An advantage of specimens killed in alco-

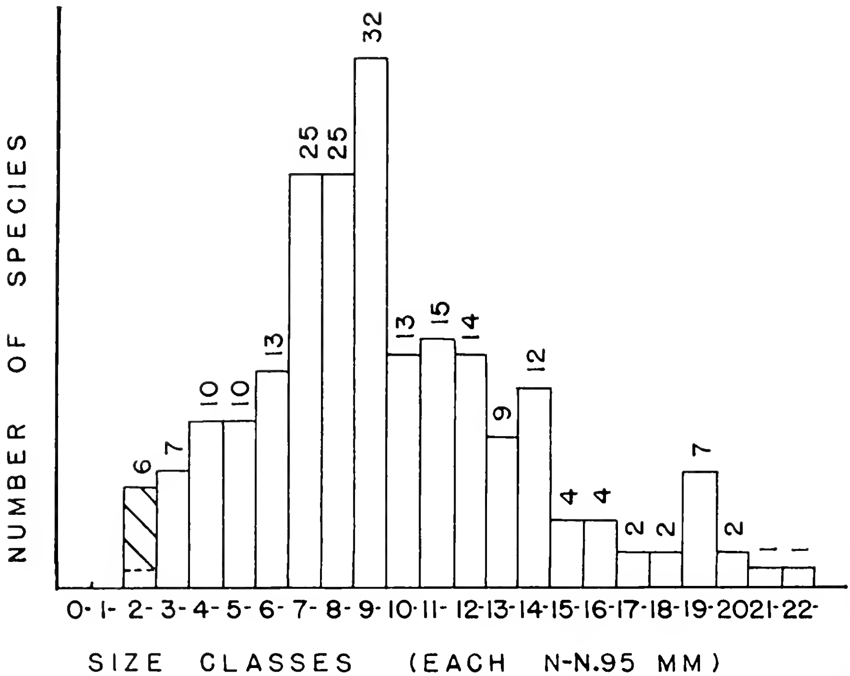


Figure 10. Histogram of size distribution of *mountain-living* Carabidae in New Guinea. Explanation as for Fig. 8. The hatched portion of the first column represents *Tachys*.

bol, as most of mine were, is that the elytra are likely to be slightly separated and the inner wings easily visible. This is not usually the case in dry-killed specimens, but if the latter are in good condition and properly mounted, it is usually possible to separate the elytra with the point of a pin and see whether or not the wings are fully developed. I have thus been able to see the wings of thousands of specimens of New Guinean Carabidae with comparatively little difficulty, and in species in which wing reduction has been detected or suspected, I have supplemented this routine examination with more careful examination, by relaxing specimens and raising their elytra. However, I have not usually extended my examination of wings to specimens collected at light, because as a rule only winged, flying individuals can come to light, so that light trap material is very deficient in flightless forms.

In discussing state of wings, I use three symbols: +w means with wings fully developed or at least long and folded at apex; ±w, wings dimorphic, full in some and reduced in other individuals; and −w, wings reduced in all individuals.

At low altitudes in New Guinea most Carabidae are +w. Many are known to fly (to light), and most probably do so. Of the 434 known lowland species (exclusive of Cicindelinae) only 17 (Table 3), or about 4 per cent, have been found to have any sort of wing reduction at low altitudes in New Guinea.[1] (Two additional species

[1] Although I have excluded tiger beetles (Cicindelinae) from my analysis and discussion of the New Guinean carabid fauna, one species should be mentioned in the present connection. It is *Tricondyla aptera* (Part I, p. 334). This is the only flightless tiger beetle in New Guinea, so far as I know. Not only is it flightless itself, but it belongs to a wholly flightless Oriental genus, and has almost surely reached New Guinea without flying. It occurs in rain forest, but not on the forest floor. It lives on the trunks of trees,

TABLE 3. LOWLAND CARABIDAE OF NEW GUINEA IN WHICH REDUCTION OF WINGS HAS BEEN FOUND

(Scaritini)

Clivina deälata (Part I, p. 372), +w and –w populations at different localities

Clivina erugatella (Part I, p. 380), +w and ±w populations at different localities

(Bembidiini)

Tachys serrula (Part I, p. 408), +w and –w populations at different localities

Tachys ambulatus (Part I, p. 425), –w at single known locality

Tachys avius (Part I, p. 426), ±w at Dobodura

(*Tachys truncatus* (Part I, p. 431; Darlington 1970: 15), apparently always +w in New Guinea but ±w in Micronesia)

(*Tachys brachys* (Part I, p. 433; present part, *Tax. suppl.*), +w in New Guinea (only 4 specimens) but –w or ±w in the Moluccas and Formosa (Taiwan)

(Pterostichini)

Lesticus politus (Part I, p. 526), 2 specimens only seen, 1 +w and 1 –w, from different localities

Platycoelus depressus (Part I, p. 534), ±w, geographic distribution of wing forms not determined

Loxandrus latus (Part I, p. 551), ±w at Doborura

(Agonini)

(No lowland species with reduced wings, although many –w in mountains)

(Oodini)

Oodes terrestris (*laevissimus* of Part III, p. 34), apparently ±w at Dobodura, but wings only slightly reduced in "–w" individuals

Oodes rossi (Part III, p. 34), single known specimen –w

(Harpalini)

Hyphaereon timidus (Part III, p. 67), ±w (wings actually polymorphic) at Dobodura; state of wings elsewhere not determined

(Lebiini)

Nototarus papua (Part III, p. 186), –w in series from Dobodura

(Pentagonicini)

Parascopodes cyaneus (Part III, p. 196), ±w at Dobodura

(Zuphiini (Leleupidiini))

Colasidia papua (present part, *Tax. suppl.*), single known individual –w

(Brachinini)

Pheropsophus aptinomorphus (Part III, p. 237), –w

Pheropsophus catulus (Part III, p. 238), –w

Pheropsophus canis (Part III, p. 238), –w

Total: 17 species, of which 10 ±w, 7 –w (so far as known); product of at least 14 separate wing-reductions; little or no radiation in –w stocks

that are +w at low altitudes are ±w on the Bismarck Range—see Table 5.) The patterns of occurrence of +w and –w individuals of these 17 species are summarized in Table 4. These 17 species represent at least 14 separate stocks, in each of which wing reduction has occurred independently. None of these stocks has radiated much at low altitudes, although speciation may have begun in the –w *Tachys* (*ambulatus* and *avius*), *Oodes*, and *Pheropsophus* (*catulus* and *canis*) (see again Table 3). It is noteworthy that no reduction of wings seems to have occurred among Agonini at low altitudes in New Guinea, although the wings have atrophied in a number of stocks of this tribe on the mountains, and although the –w agonines dominate the mountain carabid fauna of the island. In being composed almost wholly of (small) winged species, the lowland carabid fauna of New Guinea is like the faunas of some lowland areas in the continental tropics and of some other tropical islands (see fifth following paragraph).

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and it is active and conspicuous on them by day. It is about 25 mm (1 inch) long, slender, cylindrical, with large eyes and long appendages. It is strikingly antlike in appearance and movements. The exceptional success of this insect may be due to its ability to compete with large predaceous ants. It combines antlike agility and striking power (it can bite severely) with protective armor and perhaps better vision than ants have. It may be a biological example of the well-known principle, "if you can't beat them, join them." But it is exceptional, and its existence in the lowland rain forest of New Guinea emphasizes how few other carabids are flightless there.

TABLE 4. SUMMARY OF DISTRIBUTION OF +W AND –W INDIVIDUALS IN 17 LOWLAND CARABIDAE LISTED IN TABLE 3

±w populations at single localities (in single populations)	6 species
+w and –w populations at different localities	3 species
±w, but distribution of wing forms not determined	1 species
–w in all specimens seen	7 species
Total	17 species

Wing reduction among Carabidae is often followed by other structural changes, especially by narrowing of humeri and shortening of metepisterna. However, most of the lowland species (listed in Table 3) in which wing reduction has occurred either are still dimorphic (±w) or do not yet show the structural changes that tend to follow wing reduction. Of the 17 species listed in Table 3, only five begin to show the secondary structural changes (indicated above) that suggest that the insects have been flightless for a considerable time. These five are *Oodes rossi, Nototarus papua, Colasidia papua, Pheropsophus catulus,* and *P. canis.* I have collected three of these species and close relatives of the other two. All five probably live in leaf litter on the floor of rain forest. This fact suggests that selective factors are relatively favorable to flightlessness on the ground in rain forest, although the small number of species that have become flightless even there at low altitudes suggests that the selective advantage is limited. Special factors in favor of flightlessness on the floor of rain forest perhaps include the stability and continuity (both in space and time) of that habitat. Factors limiting flightlessness there may include patchiness of distributions [22] and liability to flooding. Floods often do occur on flat ground in rain forest, and Carabidae do fly to escape from them. Competition with ants, which are numerous on the ground in rain forest as well as in many other habitats in the lowland tropics (but which are fewer beside water and at high altitudes), may be an additional factor limiting flightlessness.

Known mountain-living species of Carabidae in New Guinea (found above 1000 m) total 376 species. Of these, 161 species occur also in the lowlands (below 500 m), and *all* of these species with wide altitudinal distributions are +w, except that two normally +w species of *Trichotichnus* are locally ±w on the Bismarck Range (see Table 5). There is here a correlation, perhaps to be expected, between wide altitudinal distribution and possession of functional wings.

Of the 215 species of New Guinean Carabidae found above 1000 m but not below 500 m, 69, or 32 per cent, exhibit wing-reduction (Table 5). Only one of these species is known to be ±w (*Gastragonum terrestre*, Part II, p. 226), the other 68 species being uniformly –w so far as known. In fact *Gastragonum* is the only strictly mountain-living genus of Carabidae in New Guinea in which the wings are dimorphic, most of the other strictly alticoline genera being apparently products of radiation of –w ancestors. (Exceptions are *Plicagonum*, riparian *Potamagonum*, and probably-grass-living *Maculagonum*, which are uniformly +w.) The phylogenies of the mountain-living forms have not and probably can not be fully worked out, but at least 20 different stocks (probably more) have undergone wing reduction independently to produce the –w mountain forms, and secondary structural modifications and radiation in some –w stocks indicate that wing atrophy is long-standing in many of them.

At highest altitudes, above 3000 m, only 21 species of Carabidae have yet been found in New Guinea (Table 2). Of these, 20, or 95 per cent, are –w, the only +w species on the list being *Maculagonum altipox*.

The altitudinal distribution of +w and –w Carabidae on New Guinea is consistent

TABLE 5. MOUNTAIN-LIVING CARABIDAE OF NEW GUINEA IN WHICH REDUCTION OF WINGS HAS BEEN FOUND

Scaritini)

Clivina toxopei (Part I, p. 363), –w (Australian relatives both +w and –w)

Clivina kubor (present part, *Tax. suppl.*), –w, (relatives +w)

Bembidiini)

Limnastis inops (Part I, p. 486), –w (genus includes +w species)

Panagaeini)

Craspedophorus gressittorum (present part, *Tax. suppl.*), –w (Australian species –w, some Oriental +w)

Pterostichini)

Mecyclothorax toxopei (Part I, p. 506), –w (Australian relatives both +w and –w)

Mecyclothorax sedlaceki (present part, *Tax. suppl.*), –w (see preceding species)

Lesticus (Part I, pp. 521ff; present part, *Tax. suppl.*), 5 species –w (genus includes +w and ±w species)

Rhytiferonia (Part I, pp. 533ff), entire genus (2 species) –w, (related Australian genus +w)

Prosopogmus (present part, *Tax. suppl.*), 2 species –w (genus includes +w species)

Analoma (Part I, pp. 538ff; present part, *Tax. suppl.*), entire genus (4 species) –w (relatives undetermined)

Agonini)

Notagonum ambulator (present part, *Tax. suppl.*) –w (genus otherwise entirely +w)

Gastragonum (Part II, pp. 222ff), 1 species ±w, 3 –w (genus includes +w species)

diagonum (Part II, pp. 229ff; present part, *Tax. suppl.*), entire genus (6 species) –w

Montagonum (Part II, pp. 233ff; present part, *Tax. suppl.*), entire genus (8 species) –w

Nebriagonum (Part II, pp. 235ff; present part, *Tax. suppl.*), entire genus (7 species) –w

Laevagonum (Part II, pp. 243ff; present part, *Tax. suppl.*), entire genus (7 species) –w

Fortagonum (Part II, pp. 247ff; present part, *Tax. suppl.*), entire genus (11 species) –w

(Licinini)

Microferonia baro (Part III, p. 19), –w (genus includes +w and ±w species in Australia)

(Oodini)

Oodes wilsoni (Part III, p. 35), –w (most species of genus +w

[A –w *Coptocarpus* just received from New Guinea has not yet been described]

(Harpalini)

Chydaeus (Part III, pp. 47ff; present part, *Tax. suppl.*), 2 species –w (genus includes +w and ±w Oriental species)

Trichotichnus nigricans (Part III, p. 52), ±w on Bismarck Range (+w elsewhere)

Trichotichnus altus (Part III, p. 54), ±w on Bismarck Range (+w elsewhere)

(Pengatonicini)

Scopodes altus (Part III, p. 198), –w (Australian relatives include +w and ±w species)

(Zuphiini (Lelcupidiini))

Colasida madang (present part, *Tax. suppl.*), –w (known relatives all –w, but group descended from +w stock)

Total: 71 species, of which 3 ±w, 68 –w; product of at least 22 separate wing reductions; radiation in –w stocks in some Pterostichini and especially Agonini

with distributions in some other, comparable parts of the world. Some other (but not all) tropical lowland carabid faunas are wholly or almost wholly +w, for example in the Santa Marta region of Colombia, northern South America, and on Barro Colorado Island in the Panama Canal Zone (Darlington, 1943: 41). And in the *West* Indies the situation is extraordinarily like that on New Guinea, although the Carabidae concerned are entirely separate in their immediate derivations and local evolutions. On Cuba, for example (Darlington, 1943: 49), of 144 known lowland species, almost all are +w, and of the five (3%) lowland species that do show wing reduction, four are still ±w; but –w stocks appear with increasing altitude on the mountains, and on the summit of Pico Turquino (the highest Cuban mountain, *c.* 6500 ft. or 2000 m), all seven known species are exclusively –w. I collected on Turquino myself for two weeks in 1936 and secured 459 specimens

of these seven species, every specimen –w. On Jamaica, *all* known lowland Carabidae (63 species) are +w, but again transition to –w forms occurs with increasing altitude, and above 5000 ft. (*c.* 1500 m) the ten known species are 80 per cent –w, only 20 per cent +w (Darlington, 1943: 49).

Wing atrophy of Carabidae in New Guinea is correlated not only with altitude but also with habitat. Carabids may be roughly classified as mesophiles (ordinary ground living species, called also geophiles), hydrophiles (species specifically associated with open water, especially swamps and the banks of streams), and arboreal species. (See Section [24] for further discussion of this classification of habitats.) Wing atrophy has occurred frequently among mesophiles but rarely in the other ecologic groups in New Guinea. A few –w species are or may be hydrophiles, including *Nebriagonum cephalum* and *N. percephalum* (Part II, pp. 239, 240), which live beside mountain torrents on the Bismarck Range. But, so far as I know, not one of the many arboreal Carabidae of New Guinea is –w at any altitude.

The situation among New Guinean Carabidae suggests that mutations from a long- to a short-winged condition are continually occurring at all altitudes. In the lowlands, selection apparently usually eliminates –w individuals, and most species remain +w, although wing atrophy does sometimes occur among mesophiles living on the floor of the rain forest. On mountains, however, –w mutants more often survive, species often become –w, and the –w stocks persist and sometimes radiate. This process probably occurs increasingly often with increasing altitude; it occurs most often among mesophiles, sometimes among hydrophiles, rarely if at all among arboreal Carabidae in New Guinea. In extreme cases this process has produced groups of interrelated –w species, which I have considered genera, confined to small areas in the mountains of New Guinea. Examples are *Nebriagonum* and *Laevagonum* at high altitudes on the Bismarck Range, etc. (Part II, pp. 235, 246; present part, *Tax. suppl.*).

[22] *Explantions of wing atrophy.* Wings and wing atrophy of Carabidae in various environments and on mountains and islands have been discussed by me in 1936 and 1943. I want now to summarize and apply my conclusions to the situation in New Guinea.

Their relationships indicate that most –w Carabidae on mountains in New Guinea are derived from ancestors that were +w when they reached the island [23, 88]. The –w mountain faunas are mainly products of *conversion* rather than of *concentration* (see my 1943 paper, pp. 52–53); that is, they have been produced by atrophy processes that have occurred locally, not by accumulation of –w stocks from other regions.

Certain factors should be noted that do *not* induce wing atrophy among mountain Carabidae or that are unimportant. Altitude itself (thinness of air) apparently does not induce wing atrophy or flightlessness (see my 1943 paper, pp. 50–51). Cold apparently does not directly inhibit development of wings (*ibid.*, p. 51). And exposure to wind—selection of –w forms by blowing away of +w flying individuals (Darwin's factor)—seems at best relatively unimportant (*ibid.*, p. 51), for many –w mountain-living Carabidae, including most of the ones on mountains in New Guinea, live on the ground in dense montane forest and are not exposed to winds.

Some other factors that probably do increase incidence of wing atrophy and flightlessness on mountains seem to be of only minor importance. One is freedom from flooding. In the lowlands of New Guinea, flat ground is often flooded by standing water, and winged Carabidae often do fly to escape the floods, while flightless individuals are obviously more likely to be drowned or taken by predators

(which gather over floods) before they can escape. Flood water does not stand on mountain slopes, and absence of flooding may reduce the selective advantage of flight on mountains, but it can hardly be primarily important. Another, indirect factor that increases incidence of wing atrophy and flightlessness on mountains is the increased proportion of mesophiles there. Some important classes of hydrophiles (those associated with extensive swamps and with the margins of big rivers) are absent at high altitudes, and arboreal species too are relatively few. High-mountain carabid faunas do consist mainly of mesophiles [25], and carabid wings do atrophy much more often among mesophiles than among other ecologic groups. However, wing atrophy and flightlessness are rare at low altitudes even among mesophiles, so that increase in proportion of mesophiles in mountain habitats cannot be the principal explanation of the very great increase of flightlessness with increasing altitude on the mountains of New Guinea.

There remain, I think, three factors that may be more important in favoring wing atrophy and flightlessness of Carabidae in mountain habitats in New Guinea, as elsewhere. First is an *indirect* effect of temperature. Cold, although it does not directly inhibit development of wings, does reduce ease and usefulness of flight. Cold at high altitudes, especially cold at night, probably shifts the selective advantage toward flightlessness.

A second probably important factor (inversely) correlated with altitude is intensity of competition with ants ([27], Fig. 11). Ants decrease very strikingly with increasing altitude on mountains in New Guinea (as elsewhere); they may be entirely absent at highest altitudes; and their fewness or absence may significantly reduce the selective advantage of wings and flight among mountain-living Carabidae. Perhaps this decrease should be considered a supplementary effect of cold, if cold is an important factor in reducing the incidence of ants at higher altitudes.

Third and last, but perhaps most important of all in reducing usefulness of flight and thus favoring atrophy of wings on mountains, is limitation of area. I have discussed this factor at some length in 1943 (pp. 42–44, 53). Its effect is due to the fact that Carabidae at low altitudes seem often to live on an unstable, continually changing mosaic or checkerboard of habitats, and that the principal function of wings and flight of ordinary mesophile Carabidae may be, by continual redispersals, to maintain scattered populations in large but unstable areas. This function may become even more important in the lowland tropics, where distributions apparently often are patchy even in relatively continuous habitats (Wilson, 1958). With increasing altitude in the mountains, areas become smaller. My impression (based on what I have seen in the West Indies as well as in New Guinea) is that many high-mountain species of Carabidae may be confined to areas of a few or a few hundred square miles, while many lowland species are spread over tens of thousands or hundreds of thousands of square miles, a difference of the order of 1:1,000. And the mountain areas may also be ecologically more favorable and more stable, with carabid populations denser and more stable. Under these conditions the primary function of wings and flight in maintaining discontinuous populations is probably largely lost, allowing the wings to atrophy among those Carabidae (especially mesophiles) which have no other special need to fly.

[Dr. Eugene Munroe adds (in a recent letter) that "there is very possibly also a positive selection for winglessness in conserving local concentrations of individuals sufficient to ensure a reasonable probability of mating under unfavorable conditions. Reductions of wings in arctic, mountain, insular, subantarctic and winter insects seem to be related in this respect and also

related to simplification of courtship patterns, to parthenogenesis and (in Diptera) to autogeny."]

[23] *Summary of wing state and wing atrophy.* In summary of wing state among New Guinean Carabidae: of 434 lowland species, about 96 per cent are fully winged and only about 4 per cent have dimorphic or reduced wings, and in most of these cases wing atrophy has not been longstanding and has not been followed by much secondary structural change. The 161 species that occur in *both* the lowland and the mountain faunas are all fully winged except that two species are locally dimorphic on one mountain range. But of the 215 species found only above 1000 m, 32 per cent have reduced wings, and of the 21 species known to occur above 3000 m, 95 per cent have reduced wings, and secondary structural changes and radiations indicate that many mountain-living groups have had atrophied wings for a relatively long time. However, all or almost all the wing-atrophied carabid stocks at all altitudes on New Guinea seem to have been derived by reduction of wings of ancestors which were +w when they reached the island. In explanation, I think (for reasons given in more detail in 1943) that wings of carabids atrophy in mountain habitats not primarily because flying is disadvantageous (although it may become so) but because the advantages of flight are largely lost in small but favorable and stable areas on mountains. Wings then complicate development and waste energy, so that selection favors –w individuals and evolution and radiation of –w stocks. Of course all this is still probably an extreme oversimplification. Ecologists (*e. g.*, Greenslade, 1968) are just beginning more detailed studies of the complex effects of altitude on carabid faunas.

[24] *Ecology: habitats.* Although I agree with Brass (1964: 208) that the time has perhaps arrived for leaving New Guinean ecology to the ecologists, I want to say something about major habitats in New Guinea, because knowledge of habitats is important to understanding of the carabid fauna. The information I can give is not very detailed, and some of the generalizations are only approximations, but they are substantially correct and useful. I say this in explanation, not in apology.

Several useful papers describing New Guinean vegetations are listed in my bibliography, but I have chosen to follow Brass (1941; 1964) because his system is based on practical field experience and is relatively simple and well adapted to my purposes. Actually, my classification of vegetations, although based on Brass, is even simpler than his, because I know so little of the ecology of New Guinean Carabidae that I can fit them into only a very simple system. For my purposes, I recognize the following principal vegetations, with which the distribution of Carabidae is correlated.

"Rain forest" includes coastal forest, monsoon forest, true interior lowland rain forest, and various types of wet mountain forest. It covers very large areas of New Guinea from sea level to high altitudes on the mountains, with tongues or patches of "subalpine forest" even up to 13,000 ft. (nearly 4000 m) in places. The best lowland rain forest has a high, closed canopy; vines and epiphytes are numerous but underbrush is usually scanty; and leaf debris and leaf mold are thin on the ground, except under the heads of recently fallen trees. At higher altitudes the forest trees are lower, and at highest altitudes they are extremely stunted; the trees themselves may be so low that there is not much clearance between them and the ground; and their trunks and branches are often clothed or buried in moss, especially where clouds supplement rainfall to maintain almost constant heavy moisture.

Savanna forest includes what I call "open eucalyptus forest." It is drier than rain forest and has a relatively open canopy (with the trees spaced well apart), few

or no vines or epiphytes, and usually a ground cover of grass. This kind of forest is primarily Australian, but a virtual extension of the Australian forest (presumably dating from the recent land connection) covers parts of southern New Guinea too, including the area around Port Moresby.

"Grassland" consists (to my untrained eye) of two principal types. In the lowlands, tall grass ("kunai") covers more or less extensive areas around or interspersed in the still more extensive areas of rain forest. Some of this grassland is natural: some, the result of cutting and burning of rain forest by native farmers. What seemed to me to be similar grassland, at least offering a similar habitat to Carabidae, occurs up to at least 2000 m in inhabited valleys on the Bismarck Range and elsewhere, where man has cleared the mid-altitude mountain rain forest. The second, surely natural type of grassland, with the grass much lower than "kunai" and forming tussocks, occurs above the forest line on high mountains, including the Bismarck Range.

"Wetlands" can be used to include a variety of habitats where running or standing water or simply wet ground support special vegetations and special Carabidae. Swamps are widespread at low altitudes in New Guinea, but are relatively few and small in the mountains where drainage is more rapid. The lowland swamps include large areas of sago palms, especially on the deltas of the big rivers. The enormous, spine-bearing leaves of these palms fall into the water and make working there difficult and dangerous. This habitat has therefore not been well collected for Carabidae, although it is evidently rich in subaquatic species. Other types of swamp with more diverse vegetations occur here and there, especially inland. And salt swamps, mangrove zones, and other special habitats occur along the sea coast and probably support special Carabidae, although very few of them have been collected. The edges of running water have also special

Table 6. Ecologic composition of lowland New Guinean Carabid fauna

Ecologic groups	No. of species	No. in ecologic subgroups
Fossorial (Scaritini)	27	
Mesophile	133	
Rain forest		majority
Open places		minority
Hydrophile	136	
Wet lands		105
By streams		31
Arboreal	129	
In foliage		84 (incl. 29 *Demetrida*)
Trunks/logs		45
Unclassified	9	

habitats ranging from fringes of dense forest to grass, reeds, and virtually sterile banks and bars, which may be stony, sandy, or muddy. Different habitats on the banks of large rivers, the edges and debris-blocks of smaller streams running slowly in heavy shade in rain forest, and the stony and sandy edges of rapidly running brooks all have different carabid faunas. Many of these habitats are found only or chiefly in the lowlands, but rapid brooks occur at all altitudes up almost to the peaks of the highest mountains. Besides these larger and more obvious subdivisions of wetlands, New Guinea presents an almost endless variety of wet spots sometimes only a few square meters in area: rain pools, overflow of streams, accumulations of water in holes left by the roots of fallen trees, etc., and some common carabids inhabit these places.

[25] *Ecologic composition.* The ecologic composition of the *lowland* carabid fauna of New Guinea (Table 6) is shown by figures compiled from my data sheets [16], from the column headed "Ecology." Because my information about habitats is incomplete, I have assigned some species according to the habitats of their nearest relatives; these assignments are probably correct in most cases, but perhaps wrong

in a few.[1] And in nine cases I have not wanted even to guess about the habitats of isolated species. The totals are therefore only approximations, but they are close approximations, based on my field observations.

Even when habitats are known, some species are still difficult to assign to ecologic groups. The fossorial species might be counted as hydrophiles or (a few) as mesophiles. The line between mesophiles and hydrophiles is not sharply drawn in any case; it is crossed by various species with wide ecologic ranges. The distinction between mesophiles, rotten-log forms, and tree-trunk-arboreal forms is not sharp either. Nor is the line between mesophiles and foliage-arboreal forms; it is crossed by species like *Violagonum violaceum*, which occurs in piles of dead leaves on the ground as well as in foliage. Nevertheless, these doubts and difficulties do not seriously affect the approximations given in Table 6.

In Table 6, the fossorial Scaritini are separated first, although most of them are included with the hydrophiles in statistical analyses elsewhere in the present paper. Without the fossorial forms, the lowland Carabidae of New Guinea divide almost equally into three main ecologic groups: mesophiles, hydrophiles, and arboreal forms. This is probably a fair sample of the ecologic composition of lowland carabid faunas in the wet tropics elsewhere, although hydrophiles may be relatively more numerous in some places (Darlington, 1943: 41).

In the case of the New Guinean carabid fauna, all three main categories can be usefully subdivided.

The mesophiles can be divided into rain-forest forms (the majority) and those that inhabit open places (a minority). I have not tried to give exact figures for these subgroups, because my information about the occurrence of some of the species is insufficient.

The hydrophiles divide into those that occur on wetlands in general (105 species) and those that occur only by running water (31 species). The line between these two subgroups is not sharp. However, the division is important because the streamside species are the only ones that are likely to range far up the mountain slopes. The distribution of hydrophiles depends on distribution of surface water and of special water-side habitats, and some of these habitats are independent of the type of forest cover. Some hydrophiles therefore occur in both rain-forested and opener country, and their dispersal is comparatively little affected by discontinuities in the distribution of rain forest. Also, most of them are winged and many fly actively. They are therefore likely to be good dispersers in areas (like the Malay Archipelago) where forests and opener country alternate to some extent (see [88, 91]).

Finally, the arboreal forms divide into those that live in foliage (84 species, including 29 lowland *Demetrida*) and those that live on tree trunks and recently fallen logs (45 species). Almost all these arboreal carabids occur in rain forest, of course.

With increasing altitude, the ecologic composition of the New Guinean carabid fauna changes strikingly. At higher altitudes, most Carabidae are mesophiles living in (montane types of) rain forest. Most hydrophiles have disappeared, except a few that are strictly associated with running water. And arboreal Carabidae

[1] Cases in which more or less closely related carabid species occur in different habitats include the following in New Guinea. Although most *Tachys* occur on the ground in wet places, *T. aeneus* (Part I, p. 463) occurs on *dry* ground, and *T. wallacei* (Part I, p. 479) is arboreal. Most *Oodes* are more or less aquatic, but *O. terrestris* lives in leaf litter on the ground in rain forest. And, although most *Egadroma* live in wet places, *E. robusta* (Part III, p. 71) lives on dry ground. For some examples of carabids which have made ecologic shifts within the limits of New Guinea, see [91]. All these cases of ecologic divergence have been allowed for in compiling Table 6, but some other, similar cases may still be undetected.

are reduced in numbers too, but include *relatively* more species of *Demetrida*. I know too little about the habitats of most species at higher altitudes to give exact figures.

[26] *Altitude.* Altitude affects the distribution of Carabidae in New Guinea in several ways. The change of genera and species from the lowlands to the highest altitudes is so great that, although extensive overlapping occurs at intermediate altitudes, no species are common to the lowland and highest-mountain faunas and virtually all the genera are different. (See Table 2 for composition of the highest faunas.) The only genus that is represented at all at highest and lowest altitudes is *Scopodes*, but this genus is not (in New Guinea) a regular component of the lowland fauna, and the one or two mid-altitude species of the genus that do descend to the lowlands at least locally are not closely related to the single very-high-altitude species. The effect of altitude is shown also by the striking reduction of numbers of species from the lowlands to the mountain tops (Fig. 7); by the different size distributions of lowland and mountain species (Figs. 8, 10); by the different ecologic compositions of lowland and mountain faunas [25]; and by the increased proportion of species with atrophied wings, from about 4 per cent in the lowland fauna to about 95 per cent at highest altitudes [21]. See Szent-Ivany (1965) for further notes on the vertical distribution of some beetles in New Guinea. See Greenslade (1967) for an indication of the correlation of habitats and of insect distributions with altitude in the Solomon Islands. And see Mani (1968) for a more general discussion of high-altitude insects. Note, however, that even at highest altitudes New Guinean Carabidae do not show all the modifications of alticoline forms that are found in some other parts of the world; for example, I have found no general reduction of size of individuals even at highest altitudes (cf. Mani, 1968: 58ff).

The effect of altitude on New Guinean Carabidae is apparently exerted partly indirectly, through the effect of altitude on habitats. Some species that are common in the lowlands occur also up to at least about 2000 m where forest has been cleared and where for this or other reasons habitats, including grassland, approximate lowland habitats. For example, I found the following common lowland species of Carabidae in cleared country in the Waghi and Chimbu valleys at between about 1500 and 2100 m altitude: *Tachys fasciatus* and *T. aeneus* (Part I, pp. 414, 463), *Notagonum angustellum, vile*, and *margaritum* (Part II, 133, 135, 145), *Chlaenius flaviguttatus* (Part III, p. 26), *Egadroma quinquepustulata* and *robusta* (Part III, pp. 70, 71). It seems likely that these and other winged lowland species have invaded the Waghi and Chimbu valleys from below only after the mountain valleys had been cleared. The climatic differences have not prevented the invasions, although the ecologic ranges of some of the species did apparently change with increasing altitude: some species that apparently never hide under stones at low altitudes do so in the Waghi-Chimbu area [3]. Many of the lowland species that have been found at Wau [5] at 1200 m altitude or higher have probably invaded cleared land there.

In undisturbed forest and other natural habitats the changes of carabid faunas with altitude are apparently more clear-cut. My information about occurrence of Carabidae in forest at mid-altitudes is scanty. However, I do know that all species of Carabidae found in montane forest on the Bismarck Range between about 2100 and 3000 m and all species found in open tussock-grass country above about 3000 m are different from lowland species, and many of the genera are different.

It is not yet possible to assess the relative importance of the direct effects of high-

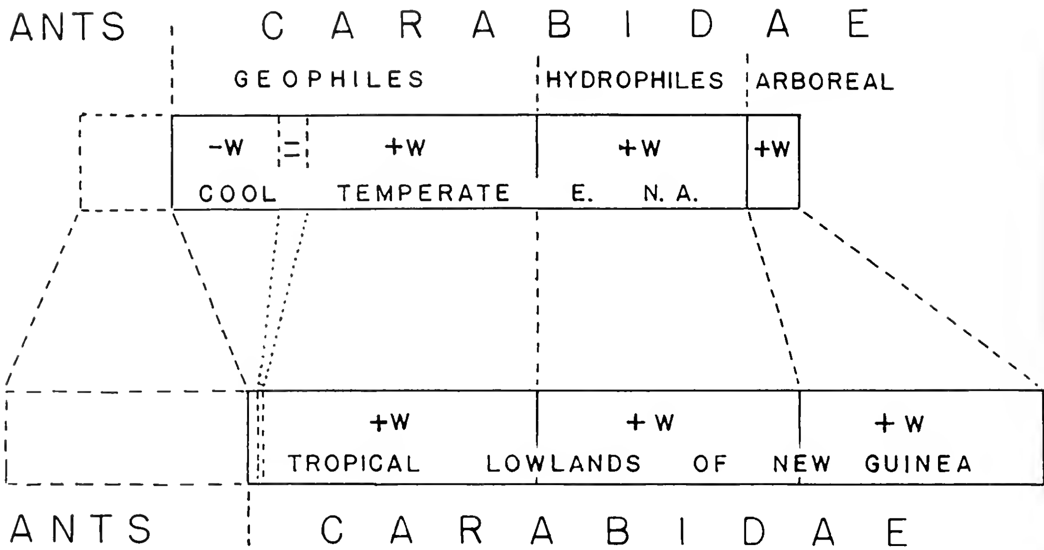

Figure 11. Diagram of (hypothetical) relation of Carabidae to ants in cool temperate eastern North America and in the tropical lowlands of New Guinea. Redrawn and modified from Darlington, 1943, p. 42, fig. 4. Diagram is intended to suggest that ants compete most severely with flightless (-w) ground-living (geophile) Carabidae; that the effects of competition are greater in the tropics than in the temperate zone; and that dominant ants replace most flightless ground-living Carabidae in tropical lowland New Guinea.

altitude climate (cold, continual dampness in some habitats, perhaps thinness of air) on carabid faunas. I can only say that, judging from the restriction of high-mountain species to special montane habitats, the indirect effects are probably more important than the direct ones. The indirect effects are probably exerted not only by control of vegetation but also by limitation of habitats on mountains (absence of large swamps, large rivers, etc.), by limitation of area on mountains (which probably affects nature of populations and, indirectly, state of wings [22]), by reduction of competition with ants [27], and perhaps in other ways.

[27] *Ants.* Ants are dominant insects, especially in the tropics, and their impact on other insects must often be tremendous. I have suggested that they may affect the size distribution of Carabidae in New Guinea [20] and that their fewness or absence at high altitudes may modify carabid faunas there [26]. Ants may also modify the ecologic composition of the lowland carabid fauna of New Guinea. This fauna, as compared with the faunas of temperate regions, is deficient in mesophiles and especially deficient in −w mesophiles, which probably compete most directly with ants. The ecologic compositions of the carabid faunas of cool temperate eastern North America and of the tropical lowlands of New Guinea are diagrammed and compared in Figure 11. The diagram is intended to suggest that the tropical fauna, which is larger than the temperate one in any case, would be still larger if it were not for the presence of ants, and that the latter take the place mainly of mesophiles and especially of flightless mesophiles.

[28] *Ecologic interactions.* The different ecologic factors discussed above do not act independently but must interact in very complex ways on carabid faunas. Major habitats and vegetations profoundly affect occurrence of Carabidae but are

themselves dependent on climate. Altitude may act partly in relatively direct ways (by reducing temperature, increasing precipitation, modifying insolation, and perhaps in other ways) and partly indirectly (by modifying habitats and vegetations). And the effect of ants varies with habitat and altitude. So, climate, habitats, altitude, and ants all interact complexly to modify the environments in which Carabidae live and to determine, directly or indirectly, how many Carabidae and what kinds of Carabidae live in different places. This statement does not do justice to the actual complexity of the environment in New Guinea. The ecologic ranges of different Carabidae on the island are surely determined by the interactions of very many factors derived from the inorganic environment, vegetations, and animal prey, predators, parasites, and competitors. Actual details are almost wholly unknown and their investigation must (as I have indicated at the beginning of [24]) now be left to the ecologists.

[29] *Ecologic ranges.* I have used the phrase "ecologic range" deliberately, rather than "niche." "Niche" is used by many ecologists, and I have used the word myself, but I think it is inaccurate and misleading. It suggests that the environment is full of pigeonholes with fixed boundaries, and that different kinds of animals and plants are in fact neatly pigeonholed in nature. Experienced ecologists know that this is not so (at least I hope they know it!), but the concept of niche sometimes confuses them just the same.

For example, ecologists sometimes speak of an island as having a certain number of niches for animals, with some of the niches unfilled, as if the niches existed before the animals were there. But if niches exist for animals at all, it is the animals themselves that make them; different kinds of animals surely in part determine the ecologic limits of other kinds. And the limits apparently change according to the number of animals present. When only a few species are present on an island, each is likely to occupy a wider segment of the environment than each will occupy when more species are present. To say that, in the first case, each species occupies several niches does not avoid the difficulty; there is no ultimate niche, no division of the environment so fine that it cannot be further divided. One might almost say that, instead of an island possessing a certain number of niches some of which may be unfilled, an island has no niches at all until animals come and define them. What the island does have is ecologic dimensions or ecologic amplitude or ecologic totality, which is not divided beforehand but which animals do divide into a few or many fractions in the course of time.

It seems to me that ecologic ranges are comparable to geographic ranges. A given piece of land—say a continent—has geographic dimensions, and is potentially able to support a varying number of species of plants and animals, each of which has a geographic range. The ranges are areas occupied by populations. They do not exist until the populations occupy them, and they often change and often overlap. Attempts have been made to divide continents into which might be called idealized (and therefore typological!) geographic ranges corresponding to climatic zones or major biomes, but (as a zoogeographer) I know that actual species' ranges often do not fit the idealized patterns very well. Similarly, to suppose that the environment can be divided into niches which exist before animals occupy them is a (typological) idealization which is likely to obscure the real facts. It is better to think of each species as having an ecologic range which is a fraction or fractions of the total environment. It is then easy to think of ecologic ranges as changing from time to time, or as being discontinuous, or as overlapping each other, as they often do. The concepts of "changing niches" and "overlapping niches" are confusing!

ZOOGEOGRAPHY: EXISTING GEOGRAPHIC PATTERNS

[30] *Geographic patterns, relationships, and origins.* Because I am a zoogeographer, especially interested in the patterns and significance of animal distribution, I shall make a geographic analysis of the New Guinean carabid fauna in much more detail than would ordinarily be attempted in a faunistic paper. In doing this, I shall begin by making a clear distinction between description of existing geographic patterns and discussion of past origins. This is just the beginning of the subdividing of the subject that is necessary to describe and understand the zoogeography of any complex fauna. Few persons, in fact few zoogeographers, fully understand how complex the subject it, or how necessary it is to recognize the complexities if zoogeographic data and analyses are to be informative and significant. I doubt if faunal relationships and other zoogeographic problems can yet be handled satisfactorily by simple numerical methods. These methods are too likely to give a superficial picture that hides more than it reveals.

The gross taxonomic compositions of major carabid faunas from the Orient (Java) to New Guinea and tropical Australia are described and diagrammed in [64] and Figure 13. Now to be considered are the finer details of distributions and relationships that underlie the gross pattern.

[31] *Existing geographic relationships: problems and procedures.* I shall begin by describing *existing* geographic patterns and relationships without intending to imply anything about past geographic origins (except sometimes parenthetically). The first question in this connection is, at what level are geographic patterns most significant: at the level of tribes, genera, or species, or of geographically separate stocks?

The choice of levels can profoundly affect the results of analysis, and the choices are often complex. For example, *Coptodera* (Part III, pp. 110ff), as I have treated it, is one genus; splitters would divide the New Guinean species among about five smaller genera; eight species of the genus occur in New Guinea; and these eight species represent seven geographically separate stocks, each with its own relationships outside New Guinea. In making faunal comparisons, should this genus be counted as one or five or eight or seven units? This is the kind of situation that numerical zoogeography too easily hides.

For another example, the genus *Demetrida* (Part III, p. 140) is represented on New Guinea by 59 known species, all apparently interrelated among themselves (apparently produced on New Guinea by radiation of perhaps only one or certainly not more than a very few ancestors). Outside New Guinea, this genus is principally Australian, but most of the Australian species are interrelated among themselves (and probably represent separate evolutionary radiations). There are certainly very few, perhaps only one, separate primary bond(s) of relationship between the New Guinean and Australian members of the genus. In making analyses and geographic comparisons, the zoogeographer must decide whether the New Guinean *Demetrida* are to be treated as 59 units with Australian relationships or as one unit with Australian relationships. This decision makes a substantial difference in the conclusions. This genus comprises nearly 9 per cent of all known New Guinean carabid species. If it is decided to count all the species separately in making faunal comparisons, this decision alone increases the "Australian" fraction by about 9 per cent of the whole fauna. But if it is decided to count *Demetrida* in New Guinea as one geographic unit, its weight in the sum of geographic relationships of the New Guinean carabid fauna is a fraction of 1 per cent. The decision how to count *Demetrida* is even more important in

analysis of the geographic relationships of the arboreal fraction of the carabid fauna, for *Demetrida* makes up nearly one-third of the arboreal Carabidae of New Guinea!

My solution of the complex problem of choice of units for zoogeographic analyses and comparisons is two-fold. First, I think it is essential to describe situations in words, giving counts of genera, species, and other units, but going beyond mere presentation of figures. I shall do this for a succession of tribes of Carabidae that occur in the Asiatic-Australian area [32ff]. And second, after the situations have been described, I think arbitrary decisions have to be made and the reasons for them given. In the present case I think the decision should be to base statistical analyses primarily on geographic units—stocks with independent geographic relationships—because they best show the degree of actual interrelationship (and also the geographic histories) of faunas. In *Coptodera* and *Demetrida* (above) the geographic units—the number of separate bonds between the New Guinean carabid fauna and other faunas—are seven and one (or very few) respectively.

Decisions about geographic relationships are complicated by differences in degree of relationship. For example, *Cillenus* (Part I, p. 399) is represented in both the Orient and Australia, but the New Guinean species is evidently more closely related to Oriental than to Australian forms. I have scored it as one (Oriental) geographic unit; and in other similar cases in which single stocks have relatives in more than one region, and in which closeness of relationship varies, I have scored only the closest relationship in each case. When, however, relationships seem equally close with (say) Oriental *and* Australian forms, I have scored both (see following paragraph). Obviously these decisions are arbitrary in principle and often also in practice.

Another complication occurs in cases like *Mecyclothorax* (Part I, p. 505; present part, *Taxonomic supplement*) and *Scopodes altus* (Part III, p. 198), in which relationships with Oriental and Australian forms seem about equally close, but in which the related forms are numerous in one region (in Australia, in the examples given) and relatively few in the other region. In such cases I have disregarded numbers and have scored geographic units solely according to apparent closeness of relationships. *Mecyclothorax* and *Scopodes altus* therefore each score one (Oriental) and one (Australian) geographic unit.

Statements of existing relationships are still further complicated by great differences in extent of the areas occupied by different genera, species, or other units. For example, *Demetrida* as a genus occurs throughout New Guinea and throughout Australia. If the New Guinean species are treated as a single geographic unit (see above), it is surely an Australian-related one. But besides the underlying Australian relationship of all the New Guinean *Demetrida*, a second link with Australia is formed by one New Guinean species which occurs also on the extreme tip of the Cape York Peninsula (see *Demetrida angulata*, Part III, pp. 143, 159). Is this to be counted as a second Australian-related geographic unit in spite of the fact that the area occupied in Australia is very small? Or take the case of *Syleter* (Part I, p. 356), a genus which ranges from the southeastern corner of Asia to the Philippines and New Guinea, with the single New Guinean species occurring again on the extreme tip of Cape York. In terms of present distribution is this to be counted as one Oriental-related unit and also as one Australian-related unit, and if so, are the two units to be given equal weight in spite of the different extents of distribution in the Oriental Region and Australia? I think that the solution of this problem too (and of others like it) is, first, to make the situation clear, and then to make an arbitrary de-

cision, and give the reason for it. In the present case my decision is to count as Australian-related only those geographic units that occur *below the Cape York Peninsula* in Australia, and to treat separately those New Guinean species that extend only to Cape York (see Table 9 [63]). This distinction seems to me to reveal important differences in distribution patterns (and to facilitate deductions about geographic histories). In the other direction, it seems to me most useful to treat as Oriental-related those geographic units that occur in Celebes or the Philippines as well as units that occur in the Oriental Region proper, but to treat separately those that occur west only to the Moluccas [62; 64, footnote].

The best way to establish a basis for zoogeographic analysis of the New Guinean carabid fauna—the way that will give the most information—is, I think, to describe the relationships of New Guinean carabids tribe by tribe, emphasizing the separate geographic units as far as they can be recognized, including but not overemphasizing counts of genera and species, and adding other significant details where possible. I can do this only because I myself did much of the taxonomic work from which the details are derived.

Most tribes of Carabidae are widely distributed. A few small tribes are localized in various parts of the world, but no tribe is confined to or represented mainly in New Guinea.

As background to understanding the relation of the New Guinean carabid fauna to other faunas, I shall begin by summarizing the distributions of certain tribes which do not occur in New Guinea but which form part of the broader pattern of geographic relationships and of change of faunas from Asia to Australia. First will be noted tribes which (in this part of the world) occur only in Asia above or chiefly above the tropics, then tribes which occur in tropical Asia and extend toward but not to New Guinea, then a few tribes that occur in both Asia and Australia but skip New Guinea, and finally tribes that (in the part of the world under consideration) occur only in Australia. And then I shall consider the tribes that are represented in New Guinea, taking them in the order of the *Coleopterorum Catalogus*, and giving in each case all the geographically significant details that I can. The nature (size, wings, etc.) of the members of each tribe will usually be noted too, and also major habitats. (Although this survey is concerned only with existing distribution patterns, some details will be referred to again in discussion of the origins and directions of dispersal of the New Guinean carabid fauna.)

[32] *Distribution of carabid tribes from Asia to Australia.* I shall now attempt to summarize, mainly by tribes, the distribution of Carabidae along a strip of the earth's surface extending almost from pole to pole, from northern Asia south and east across the Indo-Australian Archipelago (including New Guinea) to southern Australia. (See Fig. 1 for a map of the tropical portion of this area.) Details of distribution in the islands and Australia are mostly from my manuscript lists (see [4]).

Asia north of the tropics possesses several tribes of Carabidae which do not reach tropical Asia south of the Himalayas or are very poorly represented in the tropics. These northern tribes include Cychrini, Nebriini, Notiophilini, Opisthiini, Elaphrini, Loricerini, Patrobini, Amarini, and Zabrini. Two additional tribes well represented in Asia north of the tropics but not or poorly represented in tropical Asia, but present in Australia, are the Carabini and Broscini; these tribes are referred to again below. Several genera of Carabidae are outstandingly dominant in temperate Asia but absent or very poorly represented in the tropics; they include *Carabus*, *Bembidion* (which occurs also in Australia, see below), and *Harpalus*. Asia north of the tropics is notable also for possessing relatively numerous Pterostichini but rel-

atively fewer Agonini and Lebiini. The mainly northern tribes and genera of Carabidae include many mesophiles and many hydrophiles but few arboreal forms.

Tropical Asia and associated continental islands (Sumatra, Java, Borneo) possess a rich and diverse carabid fauna. Six small tribes are represented by single genera on the mainland of tropical Asia (most are represented in Africa too) but do not reach the islands; they are Enceladini, Melaenini, Anthiini, Disphaericini, Granigerini, and Idiomorphini. One additional tribe of a single genus, the Mormolycini, is confined to the Malay Peninsula, Sumatra, Java, and Borneo. Other tribes represented in tropical Asia (and more or less widely distributed elsewhere) extend for varying distances eastward across the Indo-Australian (Malay) Archipelago. The Hiletini (Camaragnathini) (one genus) have been found (in the area in question) only on the southeastern corner of Asia, Sumatra, and Borneo; the Omophronini (one genus), on the mainland of Asia and on Luzon in the Philippines (Darlington, 1967). The Siagonini (one genus) are numerous in tropical Asia and diminish eastward, the easternmost known species occurring on Java and on Mindoro in the Philippines (Darlington, 1967). And the Orthogoniini (one principal genus), with many tropical Asiatic species, diminish eastward, reaching the Philippines and Moluccas but probably not New Guinea. Some important genera of other tribes have similar patterns of diminution from tropical Asia eastward. For example, the dominant, widely distributed genus *Scarites* (large fossorial Carabidae) is well represented in the tropics of Asia, has two species in the Philippines, at least one on Celebes, and one on Timor, but does not reach New Guinea or Australia. The primarily Oriental *Trigonotoma* (rather large, ground-living, mesophile Pterostichini) reaches the Philippines and Moluccas but not New Guinea or Australia. And *Callida* (medium-sized, arboreal Lebiini) occurs in tropical Asia (and other tropical regions) and eastward to the Philippines and Celebes but not New Guinea or Australia (where its place is taken by *Demetrida*).

Asia and Australia share several tribes and important genera that are absent on most or all of the intervening islands including New Guinea. In the tribe Carabini, the genus *Calosoma* (large, ground-living, mesophile and xerophile Carabidae) is well represented in Asia above the tropics (and one or two species reach the tropical part of India), and two species occur in Australia, but the genus does not reach the southeastern corner of Asia and does not occur on the islands between Asia and Australia (except for the extension of one Australian species to New Caledonia and to the eastern Lesser Sunda Islands); this enormous gap in distribution is difficult to explain, for the genus does occur continuously across the tropics in Africa and America. The tribe Broscini (medium-sized and large, ground-living or partly fossorial, mesophile and xerophile Carabidae) includes several genera in temperate Asia and several others in southern Australia, but few enter even the edges of the tropics, and none occurs on the islands between Asia and Australia (see Ball, 1956; and Darlington, 1965: 39–42, for discussion of the genera and zoogeography of this tribe). Pogonini (rather small, ground-living Carabidae often associated with saline or alkaline habitats), too, include several genera on the mainland of Asia and several in Australia, including some in the tropics in both places, but are nearly or quite absent on the intervening islands. Two tribes, Apotomini and Amblystomini (each consisting of one principal genus of small, ground-living, mesophile Carabidae), are well represented in Asia and extend eastward across the islands to the Philippines and Celebes or the Moluccas and occur again in Australia but probably do not occur in New Guinea; both have been recorded from New Guinea, but probably in error

(Part I, p. 398; Part III, p. 19). And the following genera of small Carabidae (all including both hydrophile and mesophile species) are dominant north of the tropics, extend into (different parts of) the western Indo-Australian Archipelago, and occur again in Australia, but are absent in New Guinea: *Dyschirius* (see under tribe Scaritini, below): *Bembidion* (excluding *Cillenus*, see under tribe Bembidiini); and *Trechus* (see under tribe Trechini).

Finally, five tribes are (in the region under consideration) confined to Australia: Pamborini (one genus), to eastern Australia from the base of the Cape York Peninsula to south-central New South Wales; Migadopini, Merizodini, and Agonicini (with two to four genera each in Australia), to the southeastern corner of Australia and Tasmania; and Cuneipectini (one genus), to southwestern Australia. These tribes all consist primarily of ground-living mesophiles. They include both large (Pamborini, Cuneipectini) and small (Merizodini) forms. All existing Pamborini, Agonicini, and Cuneipectini have atrophied wings; the other tribes are winged or include winged forms.

I shall now proceed from the tribes that occur in adjacent areas but that do not reach New Guinea to tribes represented on the island itself, taking them in the order of the *Coleopterorum Catalogus* (Csiki, 1927–1933). *All* the tribes represented on New Guinea are primarily winged, although some include secondarily flightless forms. See again Figure 1 for a map of the area chiefly concerned in the following descriptions of distributions.

[Although tiger beetles (Cicindelinae) are not included in my summary and analysis of New Guinean Caribidae, their distribution may usefully be summarized parenthetically.

The tribe Collyrini (Part I, p. 334) is confined to the Oriental Region except for extensions eastward described below. The tribe consists of only two genera, both arboreal. *Collyris*, of which the species are winged and (probably) live on foliage, is rich in species throughout the Oriental Region and the Philippines, with one species on Timor and one across the central part of Wallace's Line on Celebes (and supposedly reaching the Aru Islands) but none on New Guinea. *Tricondyla*, which is flightless and lives on tree trunks, is also well represented throughout the Oriental Region; one species is endemic on Celebes and two occur on the Philippines; and one of the Philippine species extends south and east to New Guinea (Part I, p. 334), the Solomons, and Timor, and has been found in the mid-peninsular rain forest of Cape York, Australia, although it apparently does not occur in the forest on the tip of Cape York. For further comments on the distribution (and history) of this species see also footnote, section [21].

The tribe Megacephalini (Part I, p. 335) consists of terrestrial, chiefly nocturnal tiger beetles. The principal genus is *Megacephala*, which is discontinuously distributed in the warmer parts of the world. In the Asiatic-Australian area, one species extends into northern India (from the Mediterranean region); otherwise the genus is absent in Asia and absent on the islands between Asia and Australia, except that two (winged) Australian species are doubtfully recorded from southern New Guinea (Part I, p. 336); but about 20 species occur in Australia.

The tribe Cicindelini (Part I, p. 336) includes chiefly winged, terrestrial and subarboreal, chiefly diurnal tiger beetles. The tribe is worldwide in distribution. Of smaller genera, *Prothyma* is represented in New Guinea by one species with probably Oriental relationships (Darlington, 1947). *Caledonomorpha*, with two closely related species, is endemic to *eastern* New Guinea. I do not know its geographic relationships. *Distipsidera* is an eastern Australian genus of which two species have been described from southern New Guinea; these species are not directly related to each other bu

form two separate Australian geographic units; all members of the genus live on tree trunks, so far as I know. And *Therates* is an Oriental genus of which five or more species, representing at least three Oriental geographic units, occur in New Guinea, although none reaches Australia; these insects live on under-story foliage in rain forest. The single remaining genus of the tribe (so far as New Guinea is concerned) is the dominant, cosmopolitan *Cicindela* (Part I, p. 340), which includes many terrestrial as well as (in the tropics) subarboreal or arboreal species. New Guinea possesses 37 known species and three additional subspecies of this genus, representing at least eight separate geographic units (Part I, p. 341). Two of the (older?) units are Australian in present relationships. One or more stocks of very small, at least partly arboreal species have radiated on New Guinea; their geographic relationships are not clear. Two Oriental stocks are represented on New Guinea by endemic species (*maino* and *denticollis*) but do not reach Australia. *Cicindela discreta* occurs from Sumatra etc. to New Guinea and northern Australia; *C. decemguttata,* from Celebes to New Guinea etc. but not Australia; and *C. semicincta,* in New Guinea etc. and northeastern Australia and on New Caledonia.

In summary of the geographic relationships of New Guinean Cicindelinae: of Collyrini, the island possesses one Oriental species which occurs also on mid-Cape York; of Megacephalini, two Australian species (doubtfully) recorded from southern New Guinea; and of Cicindelini, *Prothyma* with one and *Therates* with at least three Oriental geographic units and *Cicindela* with apparently four Oriental and five Australian units. The presence of an endemic genus confined to eastern New Guinea and the occurrence of an extensive radiation of very small species of *Cicindela* on the island are also noteworthy. The totals are nine Oriental and seven Australian geographic units, two of the Australian units being of doubtful occurrence in New Guinea. However, the arboreal Cicindelinae that live in rain forest (*Tricondyla* and *Therates*, with together four geographic units) are all Oriental; while the terrestrial tiger beetles of New Guinea are at least as much Australian as Oriental in present relationships, and the Australian units include apparently older stocks as well as (presumably more recent) shared species.]

[33] The pantropical OZAENINI (Part I, p. 351) includes medium-sized and small Carabidae which live on the ground usually in forest and are often associated with logs and rotting wood. Four winged genera occur in the Oriental Region and one very distinct (primitive?), flightless, endemic genus is confined to eastern Australia. Two of the Oriental genera, *Danya* and *Eustra*, reach Java and Borneo, and the Philippines, but do not cross Wallace's Line to Celebes, but a third Oriental genus, *Pseudozaena*, extends eastward to New Guinea etc. but not Australia. The single species of this genus on New Guinea is the only member of the tribe there.

[34] The tribe PAUSSINI (Part I, p. 353) contains medium-sized and small, mostly winged, chiefly ground-living, primarily myrmecophilous carabids derived from Ozaenini. The tribe is pantropical, but is best represented in the main part of the Old World. Ten genera occur in the Oriental Region; all of them extend east to Java and/or Borneo and in some cases the Philippines, but none is known from Celebes; one species of the Oriental genus *Euplatyrhopalus* (Part I, p. 354) has been recorded from New Guinea, but its occurrence there is doubtful. One principal genus, *Arthropterus*, occurs in Australia; it is primitive and is not directly related to any existing Oriental genus; one species of it has been described from (southern?) New Guinea and may be the only paussid really present on the island.

[35] The tribe SCARITINI (Part I, p.

355; Part IV, *Tax. suppl.*) is the principal, dominant tribe of terrestrial-fossorial Carabidae. The tribe is worldwide in distribution although much more diverse in the tropics than in temperate regions. About 20 genera are represented in the Oriental Region and about 17 in Australia, but only three genera have been found in New Guinea. For zoogeographic purposes, the large and small members of the tribe should be grouped separately.

Oriental scaritines include about 11 genera of large and nine of small forms. Among the large forms is *Mouhotia*, a flightless genus of three species confined to the Indochinese Peninsula; this genus is apparently related to the American *Pasimachus* and perhaps more distantly the Australian carenums (Bänninger, 1950). Most of the other Oriental genera of large scaritines are confined to the mainland of Asia or to Ceylon, but *Oxygnathus* reaches Java; *Distichus*, Java and Borneo; *Thlibops*, Java and the Philippines; and *Scarites*, limits given in [32]. The small Oriental scaritines are less well known. Most genera of them are apparently localized within the Oriental Region (some are represented also in Africa), but the primarily northern *Dyschirius* reaches Java and Luzon and occurs again in Australia (but not in New Guinea), and *Syleter* and *Clivina* are discussed below.

Australian Scaritini include about 12 genera of large and five genera of small forms. The large forms are mostly "carenums," which include about 11 genera and several hundred species, all flightless, all confined to the continent of Australia and closely associated continental islands (and all probably products of radiation in Australia); a few reach Cape York, but none has yet been found on New Guinea. The carenums may be related to *Mouhotia* (above) in a general way, but probably not directly and not closely. The only other large scaritines in Australia are a few winged species of *Geoscaptus*, one of which extends to New Guinea. Small Australian scaritines include three monotypic, endemic genera as well as a few *Dyschirius* (see above) and many *Clivina* (see below); these genera are all primarily winged, although the wings have atrophied in some *Clivina*. It will be seen that there is no direct or at least no close relationship between the large Scaritini of the Oriental Region and of Australia, but that a few genera (and even some species, see below) of smaller, winged forms are common to the Orient and Australia.

New Guinea itself possesses only one Australian species of *Geoscaptus* (the only "large" scaritine on the island); one species of the African-Oriental genus *Syleter*, belonging to an Oriental species group, and extending to the tip of Cape York; and about 30 known species of the worldwide genus *Clivina*. Of the latter, *zebi, wallacei,* and *basalis* occur also in the Oriental Region and *subfusa* apparently has Oriental relationships; *basalis, sellata,* and *ferruginea* occur also in Australia, and *zebi* and *inopaca* reach Cape York; *toxopei* and *vigil* apparently have Australian relationships; and a small radiation in the "*australasiae* group" has occurred or is occurring in New Guinea, the group apparently having Australian relationships. The relationships of some of these species are doubtful, but *zebi* clearly represents an Oriental stock that extends to New Guinea and Cape York.

In summary: of large Scaritini, New Guinea possesses no Oriental and only one Australian species; but of small Scaritini, four species that occur also in the Oriental area (as here defined) and two additional Oriental relationships, and three species that occur also in Australia, two more that reach only Cape York, and three additional Australian relationships; and some radiation has occurred in one of the Australian-related stocks.

[36] The tribe BEMBIDIINI (Part I, p. 398) contains small, chiefly ground-living, often water-loving (hydrophile) carabids. There are two principal genera widely

distributed over the world including New Guinea, and a few smaller genera of which only one is represented in New Guinea.

Bembidion has very many species in the north-temperate zone including temperate Asia, fewer in south-temperate areas including five in Australia (Darlington, 1962a), and still fewer in the tropics. Several temperate Asiatic stocks of the genus extend into the western part of the Malay Archipelago, reaching Celebes and/or the Philippines (Darlington, 1959a); one species (*sobrinum* Boheman) may range more or less continuously from Asia to Australia along the Lesser Sunda Islands (Darlington, 1959a: 339–340); and one southern Australian species extends into the tropical northern part of Australia; but none of these reaches New Guinea. However, the island does have one *Bembidion* of a different stock, a member of the coastal (including intertidal) subgenus (or separate genus) *Cillenus*. This stock extends from Asia to Australia and New Zealand; the New Guinean species is related to Oriental rather than Australian forms. The absence of more-ordinary *Bembidion* in New Guinea is especially noteworthy.

The other principal genus of Bembidiini, *Tachys* (Part I, p. 400; Part IV, *Tax. suppl.*), is virtually cosmopolitan, but is best represented in the warmer regions of the world. Many species occur in tropical Asia and many in Australia, and some species range from Asia to Australia, but the Oriental and Australian *Tachys* faunas are remarkably different as wholes. New Guinea possesses 68 species, of which the geographic relationships (so far as they can be determined) are summarized in Part I, in notes under the genus and in discussions under the ten species groups. The New Guinean species include 17 that occur also in some part of the Oriental area (which for present purposes includes Celebes and the Philippines) plus three additional stocks related to Oriental forms, and eight species that occur also in Australia. (Several species that range from Asia to Australia are included in both these totals.)

The third bembidiine genus in New Guinea, *Limnastis*, is widely distributed in the Old World and reaches the West Indies and Hawaii. It is represented in New Guinea by two winged, eyed species, which range respectively from southern Asia to Australia and from southern Asia to New Guinea, and by one endemic, flightless, blind species known only from the Bismarck Range. (No aniline Bembidiini have yet been found in New Guinea, but some probably occur there. They are minute (often *c.* 1 mm long), blind carabs which usually occur in soil and which are usually obtained only by special collecting methods.)

In summary, New Guinean Bembidiini include 19 species which occur also in the Oriental area and four additional stocks with Oriental relationships, and nine species which occur also in Australia.

[37] The TRECHINI (Part I, p. 487) are small, hydrophile and geophile carabids. In this tribe, New Guinea is notable principally for what it lacks. The tribe as a whole is worldwide. Terrestrial, mesophile members of the tribe are numerous in the north-temperate zone and numerous also south of the tropics in southeastern Australia (and in southern South America); many of those in both Asia and Australia are now flightless, but winged species occur too in both places; the ancestral form(s) presumably dispersed by flight. A few species of *Trechus* have been found at high altitudes in northern Luzon in the Philippines (Darlington, 1959a), but otherwise mesophile trechines are entirely unknown in the Malay Archipelago, including New Guinea, at any altitude. Their absence in New Guinea is remarkable. However, hydrophile, stream-side trechines are sparingly represented in New Guinea. Of the widely distributed Old-World (and West Indian) genus *Perileptus*, one Oriental species reaches western New Guinea;

and *Perileptodes* is confined to New Guinea, except that one of the New Guinean species occurs also in the Solomons. It is noteworthy that *Perileptus* (above), although it occurs from Asia to western New Guinea and again in Australia, is apparently absent in the main part of New Guinea, where its place may be taken by *Perileptodes*.

[38] The tribe PANAGAEINI (Part I, p. 492; Part IV, *Tax. suppl.*) includes chiefly medium-sized, terrestrial, mesophile forms, widely scattered over the world. Geographically significant Asiatic genera not represented on New Guinea include winged *Panagaeus*, which occurs around the north-temperate zone (and in Central America and the *West* Indies) including temperate Asia and Japan but not in tropical Asia; flightless *Brachyonychus*, confined to the tropical southeastern corner of Asia; and winged *Euschizomerus*, an African-Oriental genus that reaches Java, Borneo, and the Philippines. Five genera have been found in New Guinea, all the New Guinean species being winged except the *Craspedophorus*. Of *Trichisia*, the one New Guinean species is supposedly endemic but closely related to both Oriental and Australian species. Of the tropical Oriental (and African) genus *Dischissus*, one widely distributed Oriental species reaches New Guinea. Of the African-Oriental *Microcosmodes* (*Microschemus*), one species (doubtfully assigned to the genus) occurs in New Guinea and Australia. The Oriental genus *Peronomerus* is represented in New Guinea by one Oriental and one endemic species, the latter apparently representing a second Oriental stock. And *Craspedophorus*, although well represented in both the Oriental Region (and Africa) and Australia, is known in (eastern) New Guinea by only one endemic species (a single individual) probably related to Australian rather than Oriental forms. (Although most species of *Craspedophorus* including probably all the Australian ones are now flightless, at least one of the Oriental (Philippine) species is still winged.) In summary, New Guinean panagaeines include two Oriental species and two additional species with Oriental relationships, and one Australian species and two additional species with Australian relationships.

[39] The tribe PTEROSTICHINI (Part I, p. 497; Part IV, *Tax. suppl.*) includes a large number of carabids, diverse in size, some winged and some not, many of them mesophiles, some hydrophiles, but very few arboreal. The tribe is worldwide but is both taxonomically and geographically diverse, with different genera distributed in many different patterns. The Australian genera of the tribe have been reclassified by Moore (1965), who previously (1963) transferred some supposed pterostichines to the tribe (or subfamily) Psydrini. Of the latter (primitive?) group, 18 genera are now known in Australia (Moore, 1963); *Nomius* occurs in North America, Europe and locally in Africa; and *Psydrus* is in North America. The only psydrine genus that reaches New Guinea is *Mecyclothorax*, which (for statistical purposes) I have continued to count as a pterostichine.

In the north temperate zone, mesophile pterostichines are dominant carabids; temperate Asiatic genera that do not enter the tropics are too numerous to list. On the other hand, only a few, small genera are confined to the tropical Asiatic mainland. A few additional Oriental genera reach Wallace's Line but not Celebes. *Morionidius* (two species) is known only from Tonkin (North Vietnam) and Borneo; *Diceromerus* (one species), from India to Java and Timor; *Dicaelindus* (few species), from Ceylon and Burma to Java and Borneo; and *Metabacetus* (few species) from Burma to Java, Borneo, and the Philippines. (The pterostichine genera best represented in tropical Asia and the western Malay Archipelago are actually *Lesticus, Trigonotoma*, and *Caelostomus* (mesophiles), *Abacetus* (mostly hydrophiles) and *Morion* (subarboreal), all referred to

gain below.) The mesophile genus *Trigo-otoma*, which includes some winged spe-ies and which is primarily Oriental, occurs ast to Celebes and the Moluccas but not o New Guinea.

In Australia, mesophile pterostichines are gain dominant, but the genera are almost ll different from those of Asia. Australian enera that do not reach New Guinea are oo numerous to list.

Genera of Pterostichini that do occur in New Guinea may, for zoogeographic pur-ooses, be grouped according to habitats. Most are winged; some –w species occur n primarily winged genera, and some small ndemic genera are now wholly –w, but ll are or may be derived from ancestors hat were winged when they reached New Guinea.

Ten genera of New Guinean Pterosti-hini are (or probably are) mesophiles. They include two endemic, mountain-living enera, of which *Rhytiferonia* (with two pecies) may have Australian relationships, nd *Analoma* (*Paraloma*) (with four spe-ies), Oriental relationships. A third en-lemic genus, *Haploferonia*, with one pecies, may be related to (derived from) Australian) *Loxandrus* (for which see nder hydrophiles, below). Monotypic *Brachydius* ranges from southeastern Asia o New Guinea etc. but not Australia. In he African and Oriental genus *Caelosto-mus, picipes* ranges from Asia to Australia perhaps carried by man); the other four New Guinean species are endemic but epresent at least one additional Oriental eographic unit; and one of the endemic pecies reaches Cape York. *Mecyclothorax* Part I, pp. 498, 505; present part [80], *Tax. suppl.*), is mainly Australian (and Hawaiian) but two species occur at very igh altitudes in New Guinea, and related pecies, on mountains in Java; I score this s one Australian and one Oriental geo-graphic relationship. *Catadromus* is a mainly Australian genus of very large carabids of which two *individuals* of one Australian species have been taken in New Guinea; this species occurs also on Java; I think it may be carried by man; however, in terms of present distribution, it repre-sents both one Australian and one Oriental geographic unit. *Prosopogmus* is mainly Australian; three endemic species on New Guinea comprise one Australian relation-ship; and one species is on the Moluccas. *Lesticus* is a primarily Oriental genus with eight New Guinean species; one of them occurs in Australia (and is the only *Lesti-cus* there); the other seven are endemic but their relationships are Oriental, and I count them as one Oriental unit of relation-ship. And the Oriental genus *Cosmodiscus* includes two New Guinean species which have independent relationships with Ori-ental species, and one of the New Guinean species occurs also in Australia. In sum-mary: the mesophile Pterostichini of New Guinea apparently include three species shared with the Orient plus six additional Oriental relationships; four species shared with Australia plus four additional Austra-lian relationships; and one New Guinean species that reaches Cape York.

Six genera of Pterostichini on New Guinea are primarily hydrophiles, or prob-ably so. Two of them, endemic *Homa-lonesiota* and *Nebrioferonia* (with together three species), probably live beside run-ning water; they are related to each other and to *Loxandrus* (below); I count them as one Australian unit of relationship. Of genera associated with standing water, the African-Oriental-Australian genus *Aba-cetus* is represented on New Guinea by two principal Oriental species, one of which reaches Australia; the primarily Australian *Platycoelus*, by four endemic species, probably representing at least two Australian relationships (one species reaches the Moluccas); Australian-Amer-ican *Loxandrus* (Part I, pp. 498, 549; present part [82]), by four endemic species probably representing at least two Austra-lian and one Oriental (Celebes) geographic relationships; and *Tiferonia*, by one en-demic species, the only other known species

of the genus being Oriental (Philippine). In summary: hydrophile Pterostichini in New Guinea include two Oriental species and two additional Oriental relationships; one species shared with Australia and probably at least five additional Australian relationships; and the Australian-related *Loxandrus* and its apparent derivatives, *Homalonesiota* and *Nebrioferonia* and perhaps *Tiferonia*, have apparently radiated on New Guinea, while the Oriental-related hydrophile pterostichines have scarcely done so.

The single subarboreal (bark-and-log-inhabiting) genus of Pterostichini in New Guinea is pantropical *Morion*. The two New Guinean species belong to a primarily Oriental rather than Australian group of the genus; one of the species is endemic and the other extends to Australia. In terms of present distribution, the New Guinean members of the genus score one Oriental relationship and one species shared with Australia.

The sum of existing geographic relationships of all New Guinean Pterostichini (three preceding paragraphs) is five species shared with the Orient and nine additional Oriental relationships, six species shared with Australia and nine additional Australian relationships, and one additional species extending to Cape York.

[40] The distribution of the tribe AGONINI is discussed in the present part [92]. The tribe is worldwide, better represented in the tropics than in the temperate zones, and especially dominant in New Guinea (Fig. 13 [64]), but deficient in Australia.

In the north-temperate zone, agonines are moderately numerous and include the dominant, primarily winged, hydrophile and mesophile genus *Agonum*, with numerous subgenera; the geographic limits of this genus are doubtful (because of doubt about the assignment of some tropical species), but the only subgenus that ranges far into the Oriental tropics is probably *Sericoda* (present part [80], *Tax. suppl.*), of which one Oriental species reaches New Guinea. Other agonine genera that are well represented in temperate Asia but are absent or few in the tropics include *Calathus*, *Sphodrus*, etc., and *Synuchus* (Lindroth, 1956).

Most of the agonines of tropical Asia and the western part of the Malay Archipelago are now placed in the catch-all genus *Colpodes* (Louwerens, 1953); their classification is difficult and their geographic relationships are largely unknown; the few distinct, small, Oriental agonine genera include *Onycholabis* and *Dirotus*, represented from the Malay Peninsula to Java and Borneo, with the former genus reaching also the Philippines.

The genus *Homothes* (including *Aeolodermus*) is discontinuous, with one species distributed from the Malay Peninsula to Celebes and the Philippines, none in New Guinea, but several in Australia. Otherwise, the extremely limited Australian agonine fauna includes only the endemic, monotypic, flightless *Odontagonum* (Darlington, 1956) in North Queensland, and a small number of species all of which I tentatively assign to *Notagonum* or *Colpodes*.

Known New Guinean Agonini (Part II; present part, *Tax. suppl.*) now total 21 genera and 160 species. They are medium-sized Carabidae, diverse ecologically. All those found at low altitudes in New Guinea are winged; many of the mountain-living groups now have atrophied wings (but all may be derived from ancestors that were winged when they reached New Guinea). They may be grouped according to habitat, as follows.

Mesophiles among the New Guinean Agonini include the Oriental genus *Arhytinus*, with three endemic New Guinean species, representing at least two Oriental stocks, and *Tarsagonum*, with one endemic species, the genus otherwise known only from Borneo; these two genera occur at low altitudes. Also mesophiles are certain species of the "genera of convenience"

Notagonum and *Colpodes* (of which the geographic relationships, of the mesophile species, have not been determined in detail) and some or all the species of nine endemic genera, most but not all of which are mountain-living, and most but not all of which have atrophied wings; this whole assemblage is Oriental in general relationships, but I cannot decipher the separate geographic units.

Hydrophiles among the New Guinean Agonini include at lower altitudes the single New Guinean *Lorostemma*, which is closely related to an Oriental species; some species of *Notagonum;* and the one species (several subspecies) of the endemic genus *Lithagonum;* and at higher altitudes some additional *Notagonum*; the endemic genus *Potamagonum;* and some species of the endemic genus *Nebriagonum.* Excepting the *Lorostemma* (which has been derived independently from the Orient), these agonines may all be products of the complex radiation of Agonini that has occurred on New Guinea. I cannot state their geographic ties in detail, except to repeat that they are all basically Oriental in relationships, and to add that two of the species of *Notagonum* occur also in Australia. These two are *N. submetallicum* (present part, *Tax. suppl.*) (which is distributed as if it has reached New Guinea from Australia) and *N. dentellum* (present part, *Tax. suppl.*) (which has apparently reached North Queensland from New Guinea).

Arboreal agonines in New Guinea include the African-Oriental genus *Euplenes,* with two endemic species probably representing two Oriental geographic units; the Oriental genus *Dicranoncus*, of which the one species that occurs in New Guinea ranges also from southern Asia to Australia; the subgenus *Sericoda* of the primarily northern genus *Agonum*, of which one Oriental species reaches New Guinea (present part, *Tax. suppl.*); *Violagonum*, a mainly insular genus (Darlington, MS), with the one New Guinean species occurring also in Australia; and some species of the "genus of convenience" *Colpodes*, of which three New Guinean species occur also in the Oriental area and one reaches Australia.

In summary of the geographic relationships of New Guinean Agonini: the mesophiles include four specific Oriental units of relationship; the hydrophiles, two species shared with Australia; and the arboreal forms, five Oriental species, two additional specific Oriental relationships, and three species shared with Australia. But it should be repeated again, and emphasized, that the whole diverse assemblage of Agonini on New Guinea is Oriental in general relationships, although only a few of the separate geographic units can be distinguished.

[41] The tribe PERIGONINI (Part III, p. 5) contains small, winged, mesophile carabids which live mainly in rotting logs and leaf litter. Only the worldwide genus *Perigona* (*sensu lato*) is represented in New Guinea. It includes numerous species in the Oriental Region, 14 in New Guinea, and only five in Australia (Darlington, 1964). Of the New Guinean species, five occur also in the Oriental area (which includes the Philippines) and three more have separate Oriental relationships, and one species occurs also in Australia.

[42] The tribe LICININI (Part III, p. 14; present part, *Tax. suppl.*) includes both medium-sized and small, mostly winged Carabidae, of which some are hydrophiles and some mesophiles. The tribe is nearly worldwide in distribution. A few genera, including *Licinus,* occur in north-temperate areas but do not reach tropical Asia. *Diplochila* (*Rembus*) is widely distributed in the north and in Africa and the Orient; several species reach Java, Borneo, and the Philippines, but none farther east. Several genera are confined to or occur mainly in Australia, which has more licinines than any other part of the world. Five genera are represented on New Guinea: the widely distributed genus *Badister*, by one species which occurs also

in the Orient and Australia; primarily Australian *Physolaesthus*, by one species which occurs also in the Orient; monotypic *Omestes*, by *O. torta*, which is also in the Oriental area (Celebes, Philippines); primarily Australian *Dicrochile*, by one Australian and three endemic species representing at least one additional Australian relationship; and primarily Australian *Microferonia* (Part III, p. 18; present part, [80]) by one species on the Bismarck Range in New Guinea, and one on mountains in Java. The sum of geographic units seems to me to be three species shared with the Orient (chiefly the Philippines) plus one additional Oriental relationship, and two species shared with Australia plus two additional Australian relationships. However, regardless of these unit scores, all the New Guinean licinines except the *Badister* belong to groups that are characteristically Australian rather than Oriental. (See Ball, 1959, for further discussion of the classification and distribution of some members of this tribe.)

[43] The tribe CHLAENIINI (Part III, p. 20; present part [9]) includes medium-sized (less often small or large), primarily winged, hydrophile and mesophile Carabidae. The tribe is most diverse in Africa and Eurasia. A few small genera (each with one or very few species) are confined to temperate Eurasia or the Asiatic tropics. Very small chlaeniines of the African-Oriental genus *Callistominus* reach Java, Borneo, and the Philippines (and Timor), and of the Oriental genus *Chlaeminus*, Java and the Philippines. However, only the worldwide genus *Chlaenius* (*sensu lato*) crosses the central part of Wallace's Line to Celebes, New Guinea, and Australia, and species decrease in number in this direction, Java having about 30, New Guinea 12, and Australia 10. The New Guinean species include the following geographic units (see under the species in Part III, pp. 23ff for details): six species shared with the Oriental area plus three additional Oriental relationships, and four species shared with Australia plus two additional Australian relationships. Several of the species range from the Orient to Australia or have close relatives in both, and score as both Oriental and Australian units.

[44] The tribe OODINI (Part III, p. 30; present part, *Tax. suppl.*) contains mostly medium-sized carabids most of which are subaquatic, although a few have left the water and become terrestrial. Most are winged, but some terrestrial forms have atrophied wings. Oodines occur in all the warmer parts of the world, but are relatively few in temperate areas. In the Oriental Region, *Systolocranius* (also in Africa) and *Holcocoleus* are confined to the mainland, and *Simous* (see under *Oodes laevissimus*, Part III, p. 34) ranges from India to Java and Borneo. Australia possesses numerous species of the endemic genus *Coptocarpus*, which reaches the Cape York peninsula but not New Guinea[1]. Only two genera are represented on New Guinea: *Anatrichis*, which is Oriental-Australian (and American, see [82]), and *Oodes*, which is nearly worldwide. New Guinean species include the following geographic units (see under the species in Part III, pp. 32ff): four species that occur also in the Oriental area (as here defined) and two species that occur also in Australia. The geographic relationships of the other species are undetermined.

[45] The tribe HARPALINI (Part III, p. 38; present part, *Tax. suppl.*) contains a large proportion of the common, medium-sized Carabidae that live on the ground especially in open country in all parts of the world, and the tribe includes also some common smaller forms that live especially in wet places. Most are winged. The distribution of the tribe in the Asiatic-Australian area including New Guinea is best summarized by subtribes (see Part III, p.

[1] A *Coptocarpus* has now been found in New Guinea (see *Taxonomic supplement*, footnote under Oodini).

39), although this classification is an over-simplification. One additional harpaline not belonging to any of the following subtribes should be mentioned: one species of the Old-World-tropical genus *Pachytrachelus* (subtribe Pachytrachelina; Csiki, 1932: 1082) ranges from India etc. to Australia perhaps along the Lesser Sunda Islands, although the genus does not occur in New Guinea.

Harpalini of subtribe Anisodactylina are chiefly medium-sized mesophiles. The principal genus in the north-temperate zone is *Anisodactylus* (*sensu lato*), which is Holarctic; it enters the edge of the tropics in southeastern Asia but does not reach the tropical islands; however, two related, monotypic, primarily insular genera, *Rhysopus* and *Harpalomimetes*, do reach Java and/or Borneo (Wallace's Line). Also in this subtribe is *Chydaeus* (Part III, p. 47; present part, *Tax. suppl.*), which occurs at high altitudes on the Himalayas and on mountains in Formosa, Sumatra, Java, the Philippines, and New Guinea, but does not reach Australia. It has apparently "mountain hopped" some 4,000 miles (more than 5,000 km), by steps, from the mountains of Asia across the Malay Archipelago (see [80]). Three other genera of Anisodactylina are best represented in Australia but reach New Guinea and extend westward into and across the Malay Archipelago, chiefly in relatively open country including open eucalyptus woodland, although some species occur in rain forest too. Of these primarily Australian genera, *Gnathaphanus* has five species in New Guinea all of which occur also in Australia and two of which reach only the southern edge of New Guinea, the others reaching (respectively) West New Guinea, the Malay Peninsula, and India; *Diaphoromerus*, two endemic species in New Guinea closely related to (different) Australian species, one of the New Guinean species reaching also the Moluccas; and *Hypharpax*, one New Guinean species which apparently occurs also in northeastern Australia and extends west to Java and Sumatra. The geographic units of New Guinean Anisodactylina are therefore three species that occur also in the Orient plus one additional Oriental relationship, and six species that occur also in Australia plus two additional Australian relationships. (However, excepting *Chydaeus*, the Anisodactylina that reach New Guinea are all primarily Australian, and they show an exceptionally clear pattern of spread westward across the islands.)

Harpalini of subtribe Pelmatellina are represented in New Guinea by only three small, endemic, water-loving species of the diverse Australian genus *Lecanomerus* (Part III, p. 45); they may all be derived from one ancestor and I count them as one Australian geographic relationship.

Harpalini of subtribe Harpalina are (in the area under discussion) primarily Asiatic-Oriental and do not occur in Australia at all, except that one or two genera reach just the northern edge of the continent. *Harpalus* itself is a dominant Holarctic genus which occurs south to Java (one species) but does not cross Wallace's Line. *Oxycentrus* reaches at least Celebes; *Dioryche*, at least Celebes and Timor; but these few details do not do justice to the numbers and complexity of limits of the Oriental Harpalina. Members of this subtribe are dominant on the ground in New Guinea, especially in rain forest, but the New Guinean Harpalina represent merely the fringe of the much richer Asiatic-Oriental fauna. The principal genus of the subtribe that does reach New Guinea is *Trichotichnus* (Part III, p. 48), with 14 species on the island showing at least three separate Oriental relationships ("*Carbanus*," "*Lampetes*," and the others). *Harpaloxenus*, with five species on New Guinea, is apparently closely related to *Trichotichnus* and counts as at least one additional Oriental relationship. *Lyter* is a new, endemic, monotypic genus confined to New Guinea (and perhaps derived from *Trichotichnus* on the island). *Coleolissus* has two en-

demic species on New Guinea representing perhaps only one Oriental stock; one of the species of *Coleolissus* is represented on Cape York. Finally, *Platymetopus* is represented on New Guinea by one Oriental (Philippine) species that apparently reaches only western New Guinea. In summary: the geographic units of New Guinean Harpalina are one species shared with the Orient (Philippines) and at least eight additional Oriental relationships, and one New Guinean species reaching Cape York. (This is a remarkably clear pattern of multiple dispersal of a dominant Asiatic-Oriental group south and east across the Malay Archipelago.)

Harpalini of the subtribe Acupalpina are relatively small forms most of which live in wet places on the ground. Their generic classification is not very satisfactory; all the genera represented in New Guinea are widely distributed at least in the Old World, but their zoogeographic limits (except as they concern New Guinea) need not be discussed here. Of *Egadroma*, New Guinea possesses four species, of which three apparently occur also in both the Orient and Australia and the fourth is closely related to an Oriental species (present part, *Tax. suppl.*). *Anoplogenius* is represented in New Guinea by one species that probably ranges from the Orient (Sumatra) to Australia; *Stenolophus*, by two species both probably present in the Oriental area and in Australia. Finally, the six New Guinean *Acupalpus* include apparently two species that occur also in the Orient plus two additional Oriental relationships, and one species that occurs also in Australia plus two additional Australian relationships (see details given in *Notes* under the species, Part III, pp. 73ff). The sum of geographic units of New Guinean Acupalpina is therefore eight species plus three additional relationships Oriental, and seven species plus two relationships Australian. (But the pattern as a whole is clearly one of multiple dispersal of Acupalpina from the Orient to New Guinea and Australia.)

The sum of geographic units of New Guinean Harpalini of all subtribes is 12 species shared with the Orient plus 12 additional Oriental relationships, 13 species shared with Australia plus five additional Australian relationships, and one additional species reaching Cape York.

[46] The small, pantropical tribe ANAULACINI (Part III, p. 76) contains small, winged, mesophile carabs which usually live in leaf litter on the ground in rain forest. New Guinea possesses four genera: *Anaulacus* is represented by one species, which is widely distributed also in both the Orient and Australia; *Caphora*, by one Oriental species that has been found also on the tip of Cape York; *Aephnidius*, by one Oriental species that does not reach Australia; and *Odontomasoreus*, which is endemic and of unknown relationships, by one species and one additional subspecies. The geographic units are therefore three species that occur also in the Orient, one also in Australia, and one additional occurrence on Cape York. The few additional members of the tribe that occur in the Orient are geographically insignificant; no additional ones occur in Australia.

[47] The CYCLOSOMINI (Part III, p. 78) is another small tribe of rather small, winged Carabidae widely distributed in the warmer parts of the world. Of the few genera represented in tropical Asia, *Tetragonoderus* (which is widely distributed in the Old World and the Americas) and *Cyclosomus* (which is African and Oriental) reach Java and the Philippines but not Celebes. These genera are terrestrial. In Australia the tribe is represented only by numerous species of *Sarothrocrepis*. Most of them live on shaggy tree trunks but one group of small species is foliage-arboreal, and this group is represented by endemic species on New Guinea, Java, the Philippines, and some Lesser Sunda Islands. The New Guinean species is ap-

parently closely related to both Australian and Oriental (Javan, etc.) forms.

[48] The tribe LEBIINI (Part III, p. 80, present part, *Tax. suppl.*) is, among Carabidae, equalled in number of species on New Guinea only by the Agonini. However, the Lebiini are far more numerous and diverse at low altitudes on the island and far more complex in their discernible geographic relationships. Most tropical lebiines are arboreal, and all the 160 New Guinean species except *Nototarus papua* are winged. In discussing the New Guinean forms in detail (below) I shall group them by major habitats. First, however, I shall state briefly the distribution of genera that occur in neighboring regions but do not reach New Guinea. The Oriental forms are especially numerous and significant, but I cannot group them by habitats, because I do not know the habitats of many of them.

The north-temperate zone possesses comparatively few Lebiini. Of the genera that do occur in temperate Asia, the most important is Holarctic, terrestrial *Cymindis*, a genus well represented in temperate Asia but which scarcely enters the Asiatic tropics.

Tropical Asia possesses relatively more Lebiini, but only half a dozen or so small genera of the tribe are actually confined to the tropical Asiatic mainland.

A much larger number of genera occur on the Malay Archipelago. Some of them are represented on the mainland of tropical Asia too or even in Japan, and some reach New Guinea (as detailed below), but about 15 do not reach New Guinea. Of these 15 genera that are represented in the western part of the Malay Archipelago but that do not reach New Guinea, 12 reach Java and/or Borneo (and sometimes also the Philippines and/or some of the Lesser Sunda Islands) but (so far as known) do not cross the central part of Wallace's Line to Celebes. These are mostly small genera of one or very few species; they include *Allocota* (three species), distributed from Burma to Java, Borneo, and the Philippines; *Lebidia* (four species), from eastern Asia and Japan to Java; and *Dromius*, with many species in the northern hemisphere, fewer in tropical Asia, and one species (probably undescribed) on Sumatra and two on Java.

Two other, important genera of Lebiini do cross Wallace's Line but do not reach New Guinea: *Lioptera*, with about eight species, is distributed from southeastern Asia and Japan to Borneo, Celebes, and the Philippines; and *Callida*, well represented in all the warmer parts of the world *except* the Australian region but including tropical Asia, reaches Java, Borneo, Celebes, and the Philippines, and also some of the Lesser Sundas.

Australia has comparatively few Lebiini, and many of those that do occur in Australia are the same as or related to New Guinean species and are noted in my enumeration (below) of the geographic relationships of New Guinean genera. Additional significant lebiines in Australia include *Philophloeus*, with many species occurring through most or all of the continent, chiefly on the shaggy trunks of eucalypts and other trees. *Agonochila* and *Demetrida* are numerous in Australia (and have apparently radiated separately there) chiefly on tree trunks, but are represented on New Guinea too, of course. And *Phloeocarabus* and *Trigonothops* (these two genera I think mainly on tree trunks) and *Nototarus* and *Anomotarus* (I think chiefly on the ground) are well represented in Australia too, although present also in New Guinea. Other genera of lebiines in Australia seem geographically unimportant.

New Guinea has representatives of 32 genera of Lebiini, and the geographic relationships even of some single genera are complex. In discussing their relationships, I shall divide them into ecologic groups comparable to those into which I have divided some preceding tribes, although the basis of division is not quite the same. Among New Guinean Lebiini few genera

are terrestrial, none is hydrophilous, but many are arboreal; and the arboreal forms are divided, those that live on tree trunks and those that live in foliage being grouped separately. And several genera which do not fit into this ecologic classification or of which the habitats are unknown are noted last of all.

Terrestrial (mesophile) or probably terrestrial Lebiini in New Guinea include one species of the Asiatic-Australian genus *Lachnoderma*, the New Guinean species occurring also in Australia; one Oriental species of the Oriental genus *Sinurus;* one endemic species of *Peliocypas*, this being the easternmost representative of a diverse Oriental group; one Oriental-Australian species of *Syntomus*; two species of *Microlestes*, one with Oriental and one with apparent Australian relationships; two endemic species of *Apristus*, the easternmost representatives of this African-Oriental (and North American) genus, representing perhaps a single Oriental geographic unit; one endemic species of the Australian genus *Nototarus;* eight endemic species of the Asiatic-Australian genus *Anomotarus*, the geographic relationships of one of the species being Oriental and the others undetermined (except that one extends to the Moluccas); and one Oriental species of the Oriental genus *Omobrus*. In summary, the terrestrial or probably terrestrial Lebiini of New Guinea include three species that occur also in the Orient plus four additional Oriental relationships, and two species that occur also in Australia plus two additional Australian relationships.

New Guinean Lebiini that live mainly *on tree trunks* and on fallen logs include one endemic species of the Oriental genus *Stenotelus;* one Oriental species of *Miscelus* that has been found also in mid-Cape York, and two endemic species of the same genus representing at least one additional Oriental relationship; nine species of the mainly New Guinean genus *Minuthodes*, one of the new Guinean species having a relative in the Orient (Celebes) and one a relative in Australia; 14 species of the widely distributed tropical genus *Catascopus* related as detailed below; one endemic species of *Pericalus*, the easternmost (except for another endemic species on New Britain) of a species-rich Oriental genus; eight species of the widely distributed genus *Coptodera*, detailed below; one endemic species of the Oriental genus *Mochtherus;* and two species of the primarily New Guinean genus *Stricklandia*, one of the New Guinean species reaching the Moluccas, with a closely related species in Australia. In more detail, the New Guinean *Catascopus* (Part III, pp. 101ff, see especially *Notes* under the genus) include *elegans*, which ranges from tropical Asia to northern Australia; *smaragdulus*, from tropical Asia to New Guinea and mid-peninsular Cape York; *facialis*, from tropical Asia to *Western* New Guinea; *laevigatus*, which occurs also in the Moluccas and has a close relative in Australia; and *aruensis*, which occurs also in mid-peninsular Cape York. The geographic units of the genus listed in the preceding sentence are three species shared with the Orient; and one species shared with Australia, one additional Australian relationship, and two additional extensions to Cape York. (Nevertheless, *Catascopus* is most diverse in the Orient; several additional stocks have probably reached New Guinea in the past, although I cannot now distinguish them, and *all* the few Australian species seem to represent more or less recent invasions from New Guinea.) *Coptodera* (Part III, p. 110ff) includes endemic *grossa*, with no recognized close relatives; *cyanella, lineolata, eluta,* and *oxyptera*, all of which occur also in some part of the Oriental area; *ornatipennis*, which occurs also in the Moluccas and has a relative in Celebes (Oriental area); and *papuella* and *wau*, which together form one Australian-related unit: total units in this genus: four species that occur also in the Oriental area plus one additional Oriental relationship, and one Australian re-

lationship. Geographic units for all the tree-trunk-living New Guinean Lebiini are eight also-Oriental species plus six Oriental relationships, and one also-Australian species plus four Australian relationships, and three additional species reaching Cape York.

Arboreal Lebiini that probably live mainly *in foliage* on New Guinea include the following: three endemic species of the Oriental genus *Aristolebia* perhaps representing one Oriental stock, one of the species occurring also on the tip of Cape York; seven species of the worldwide genus *Lebia*, their geographic relationships detailed below; one endemic species (the easternmost of the genus) of the Oriental genus *Physodera;* one endemic species of the mainly Oriental genus *Holcoderus*, the New Guinean species having close relatives in both the Orient and Australia; monotypic *Oxydontus*, the one species occurring also in the Orient; 13 species of the mainly Oriental *Dolichoctis*, related as described below; monotypic *Celaenephes*, the one species occurring also in the Orient and Australia; three species of the mainly African-Oriental *Parena*, one of the species occurring also in the Orient, one also in Australia, and one in the Orient and Australia; and 59 known endemic species of the otherwise mainly Australian *Demetrida* (all perhaps derived from one Australian-related stock) with one of the New Guinean species found also on the tip of Cape York. In more detail, the New Guinean *Lebia* include *karenia*, which is also Oriental; *melanonota* (present part, *Tax. suppl.*) which is Oriental and Australian; *papuella*, with a close relative in Australia; and additional species of which the relationships are undetermined or are with other New Guinean species. And of *Dolichoctis*, *striata* ranges from southern Asia to New Guinea and Australia; *microdera*, from Sumatra to New Guinea; and the remaining 11 New Guinean species of the genus, all members of or perhaps derived from the *aculeata* group, include one species (*aculeata*) that occurs also in the Oriental area (Celebes) and reaches mid-peninsular Cape York, and at least one additional Oriental relationship. The sum of geographic units of the foliage-living New Guinean Lebiini is nine species that occur also in the Orient plus four Oriental relationships, and five species that occur also in Australia plus three Australian relationships and three additional occurrences on Cape York.

Besides the Lebiini listed in preceding paragraphs, four lebiine genera of which I do not know the habitats occur in New Guinea. These genera are probably arboreal, but I do not know whether (in New Guinea) they live on tree trunks or in foliage. *Agonochila* is a primarily Australian genus with seven small endemic species in New Guinea representing perhaps only one Australian-related stock; most members of this genus in Australia live on tree trunks, but a few small tropical Australian species inhabit foliage, and the New Guinean ones may do so too. *Minuphloeus* is a monotypic genus confined to New Guinea; its relationships and habitat are unknown. *Phloeocarabus* is primarily Australian but is represented on New Guinea by one species that occurs also in Australia and one that is endemic and represents a separate Australian-related unit. And *Trigonothops* is primarily Australian but includes one New Guinean species closely related to an Australian species. The geographic units of these four genera total one species shared with Australia plus three Australian relationships.

Finally, as far as Lebiini are concerned, two genera are represented in New Guinea by single species that are carried by man and that cannot be placed in the preceding habitat classification. They are *Anchista* and *Endynomena*, each represented in New Guinea by one species that has been found also in the Orient but not in Australia. (*Plochionus pallens*, if it turns up in New Guinea, will be a third man-distributed lebiine in New Guinea.)

TABLE 7. SUMMARY OF GEOGRAPHIC RELATIONSHIPS OF NEW GUINEAN LEBIINI

Habitat	Species also Or.	Additional Or. units	Species also Au.	Additional Au. units	Additional to C. York
Ground	3	4	2	2	–
Trunks	8	6	1	4	3
Foliage	9	4	5	3	3
Prob. arb.	–	–	1	3	–
Man-carried	2	–	–	–	–
Total	22	14	9	12	6

Table 7 sums up the geographic relationships of New Guinean Lebiini.

The distribution and relationships of Lebiini from Asia to Australia may be summarized as follows. The tribe is relatively poorly represented (and chiefly terrestrial) in temperate Asia. It is better represented (and more arboreal) in tropical Asia, with some small genera confined to the tropical Asiatic mainland and others, including larger genera, extending onto the Malay Archipelago for various distances. The lebiines of the Western (Oriental) part of the archipelago are numerous and include about a dozen (mostly small) genera that reach Java and/or Borneo but do not cross Wallace's Line to Celebes, and also two important genera that do extend to Celebes but not New Guinea. The Lebiini of New Guinea are numerous too, and include 22 species that occur also in the Oriental area plus at least 14 Oriental relationships, nine species that occur also in Australia plus at least 12 Australian relationships and six additional species that reach Cape York. Some New Guinean genera are represented also in Australia, but additional Australian genera are few, the important ones being mostly tree-trunk-living or terrestrial.

This whole main pattern of distribution from Asia to Australia reflects the fact that Lebiini are primarily arboreal Carabidae, far more numerous in the complex arboreal habitats of tropical rain forest than they are in thinner and less complex temperate woodlands.

The localization of a number of small genera toward the Oriental end of the Malay Archipelago and the extensive radiation in several genera in New Guinea (see below) suggests that, although some *species* have been able to disperse from southern Asia to Australia, some other lebiines have dispersed less effectively than might have been expected of such active, winged Carabidae. Their dispersal may have been limited either by limitation of their power of dispersal or by discontinuities in the distribution of the rain forests in which most of them live. It is noteworthy that the lebiines that have radiated in New Guinea have diverse geographic relationships: the foliage-living *Demetrida* (59 species on New Guinea derived from one or a few ancestors!) is Australian-related; the foliage-living *Dolichoctis* and tree-trunk *Catascopus* (in both of which moderate radiations have occurred in New Guinea) are primarily Oriental in relationships; and the foliage-living *Dicraspeda* (six New Guinean species) and tree-trunk *Minuthodes* (nine New Guinean species) are primarily New Guinean. The only ground-living lebiine genus in which radiation seems to have occurred on New Guinea is *Anomotarus* (eight New Guinean species, seven of them perhaps products of local radiation); the primary geographic relationship of the New Guinean members of this genus is undetermined.

[49] The small tribe PENTAGONICINI (Part III, p. 191) includes only four genera, of which one is confined to New Zealand, the other three being represented in New Guinea. *Pentagonica* occurs in all

the warmer regions of the world and includes six species on New Guinea: two of them apparently range from southern Asia to Australia; two more, from southern Asia to New Guinea and Cape York; and two are endemic. The one known species of *Parascopodes* occurs in eastern New Guinea and northern Australia. And *Scopodes* is divisible into two stocks: one stock is mainly Australian but includes one species at very high altitudes on the Snow Mountains of New Guinea and one on high mountains in Java; and the other stock is confined to New Guinea and includes seven species which are perhaps all products of one (Australian-related) radiation. Pentagonicines are small Carabidae. The New Guinean species of *Pentagonica* are arboreal, in foliage; of *Parascopodes*, ground- or grass-living; and of *Scopodes*, ground- or log-living.

[50] The small, African-Oriental tribe HEXAGONIINI (Part III, p. 202; present part, *Tax. suppl.*) includes two genera in the Orient: *Dinopelma* (about 11 species) is apparently confined to the western part of the Malay Archipelago, with several species on Java, Borneo, and the Philippines but none on Celebes; *Hexagonia* (which occurs also in Africa) is rather diverse in the Orient; two Oriental stocks are represented in New Guinea by single endemic species; and one of these stocks has one endemic species in Australia, too. The members of this tribe that I have collected are rather small, winged Carabidae which live under the leaf sheaths of tall grasses.

[51] The tribe ODACANTHINI (Part III, p. 203), which is worldwide in distribution, includes small and medium-sized, winged carabids of which some are terrestrial and some arboreal, some of the subarboreal forms being also hydrophilous. Few occur in temperate Eurasia. The Orient possesses many, diverse species of the worldwide genus *Colliuris* (see below) and representatives of a few smaller genera (some named below). New Guinea has eight genera, 19 species, rather diverse in ecology and in geographic relationships (see below). And Australia has several small endemic genera as well as representatives of several of the genera that occur on New Guinea.

New Guinean Odacanthini are as follows. The genus *Colliuris* (see above) includes four species in New Guinea, of which one occurs also in the Orient, one is endemic but related to an Australian species (it and the preceding probably live in grass especially in wet places), and two are endemic but probably represent one Oriental stock, and one of these species occurs also on the tip of Cape York (these species live on or near the ground in wet places). Of the Oriental-Australian genus *Casnoidea*, only two species surely occur in New Guinea: one is endemic, and one occurs also in Australia (the members of this genus live in grass and reeds over water). The one known species of *Basisticus* occurs in northeastern Australia and southern New Guinea (it lives on the ground in more or less open country). *Clarencia* is an Australian genus with two species on New Guinea: one occurs also in Australia, the other is endemic but Australian-related (they live on or near the ground in wet places). *Dicraspeda* is primarily New Guinean, with six rather diverse species; three geographic stocks can be distinguished; *brunnea* ranges from Java and the Philippines to New Guinea and northeastern Australia; *longiloba*, *dubia*, and *bispinosa* are endemic and perhaps represent one stock which is confined to New Guinea except that *longiloba* reaches New Britain and *dubia* Cape York; and *quadrispinosa* and *violacea* are related to each other (and probably derived from the same stock as the preceding) and are confined to New Guinea except that one or both reach the Moluccas, New Britain, and/or the Solomons. (All species of this genus live in under-story foliage of rain forest.) One Oriental species of the African-Oriental genus *Lachnothorax* reaches

New Guinea but not Australia (I think it lives beside running water). One New Guinean species is tentatively assigned to the Australian genus *Eudalia* but may also have Oriental relationships (this is probably water-loving too). And *Dobodura* is a monotypic genus confined to New Guinea but perhaps derived from the Australian *Eudalia* (it lives among stones beside turbulent brooks). The sum of geographic units of the New Guinean Odacanthini is three species that occur also in the Oriental area plus one Oriental relationship, and four species that occur also in Australia plus four Australian relationships, and two additional species reaching Cape York.

[52] The DRYPTINI (Part III, p. 216) is a small tribe of medium-sized, usually winged Carabidae which usually live on the ground or in grass, I think. Of this tribe, the widely distributed, terrestrial genus *Galeritula* (Reichardt, 1967) crosses Wallace's Line to Celebes; the Old-World (and Brazilian) genus *Drypta* is represented in New Guinea by two endemic species probably related to different Oriental forms, by one Australian species which reaches only the southern edge of New Guinea, and by one additional endemic species; and the Old-World genus *Desera* includes one New Guinean species which is endemic (except that it reaches also New Britain and New Ireland) but closely related to species in both the Orient and Australia. Besides these, the tribe contains only a few small genera none of which occurs in the area under consideration except that *Pseudaptinus* (*Thalpius*), a genus of small terrestrial dryptines widely distributed in the Americas, has also one species in Australia.

[53] Of the small tribe ZUPHIINI (Part III, p. 218; present part, *Tax. suppl.*) which includes small, mesophile and hydrophile carabids, New Guinea possesses one endemic species of the worldwide genus *Zuphium* and one Australian species of the same genus that reaches only southern New Guinea; four species of the African-Oriental genus of *Planetes*, one being also Oriental and one also Australian; and two endemic species of *Colasidia* representing one Oriental stock. The few other (small) genera of the tribe include Oriental *Agastus*, which reaches Java, Borneo, and the Philippines, and *Acrogenus*, confined to Australia.

[54] Of the small, Oriental-Australian tribe HELLUODINI (Part III, p. 222), which includes only one principal genus of medium-sized, winged, mesophile carabids, New Guinea possesses nine species of *Pogonoglossus*. The species of this genus are moderately diverse in the Oriental Region as well as New Guinea, less diverse in Australia. All the New Guinean species are endemic, and I cannot determine their individual relationships outside New Guinea. The few species that I have collected were found in leaf litter on the ground in rain forest.

[55] The tribe HELLUONINI (Part III, p. 228; present part, *Tax. suppl.*) includes medium-sized (rarely large), usually winged, ground- or tree-trunk-living Carabidae widely distributed over the world. The genus *Omphra* is confined to India and Ceylon; monotypic *Colfax*, to the tropical mainland of Asia; the African-Oriental genus *Macrocheilus* reaches Celebes; and one species of the Oriental genus *Creagris* extends to New Guinea and Australia. A dozen additional Australian genera form a special Australian group of the tribe; of these genera, three are represented in New Guinea by single Australian species (two of these reach only southern New Guinea), and *Helluonidius* includes four New Guinean species which are diverse but may represent one Australian-related stock. *Helluopapua* (two species) is endemic but may represent the same stock. I therefore score New Guinean Helluonini as including one Oriental species, four species that occur also in Australia, plus one Australian relationship.

[56] The BRACHININI (Part III, p. 234; Erwin, 1970) are medium-sized and

TABLE 8. SUMMARY OF GEOGRAPHIC RELATIONSHIPS OF NEW GUINEAN CARABIDAE PROPER BY TRIBES

Tribe	Ecology	Or. spp. (+ Or. rel.)	Au. spp. (+ Au. rel.)	Cape York
Ozaenini	Meso	1		
Paussini	Meso	(1)	(1)	
Scaritini				
large	Hydro		1	
small	Hydro+	4 (2)	3 (3)	1 [1]
Bembidiini	Hydro+	19 (4)	9	
Trechini	Hydro+	1		
Panagaeini	Meso	2 (2)	1 (2)	
Pterostichini	Meso	3 (6)	4 (4)	1
	Hydro	2 (2)	(5)	
	Subarb	(1)	1	
Agonini	Meso	(4)		
	Hydro	2		
	Arb	6 (2)	3	
Perigonini	Meso (incl. logs)	5 (3)	1	
Licinini	Hydro, Meso	3 (1)	2 (3)	
Chlaeniini	Hydro, Meso	6 (3)	4 (2)	
Oodini	Hydro	4	2	
Harpalini				
Anisodactylina	Meso (open)	3 (1)	6 (1)	
Pelmatellina	Hydro		(1)	
Harpalina	Meso+	1 (8)		1
Acupalpina	Hydro+	8 (3)	7 (2)	
Anaulacini	Meso	3	1	[1]
Cyclosomini	Arb	(1)	(1)	
Lebiini				
	Ground	3 (4)	2 (2)	
	Trunks	8 (6)	1 (4)	3
	Foliage	9 (4)	5 (3)	3
	Prob. arb		1 (3)	
	Man-carried	2		
Pentagonicini	Arb, meso	4 (1)	3 (2)	2
Hexagoniini	Arb	(2)	(1)	
Odacanthini	Arb, meso, hydro	3 (1)	4 (4)	2
Dryptini	Arb	(3)	1 (1)	
Zuphiini	Meso	1 (1)	2	
Helluodini	Meso	–	–	
Helluonini	Meso (+?)	1	4 (1)	
Brachinini	Meso, hydro	(2)	1	
Pseudomorphini	Arb	(1)	(5)	
		104(69)	69(51)	—
		173	120	13 (2)

small, mostly winged, ground-living, hydrophile and mesophile "bombardiers." Most of those in the north-temperate zone are species of *Brachinus* (see below). Small forms of the African-Oriental genera *Styphlomerus* and *Mastax* reach Java and the Philippines (*Styphlomerus*, Timor too) but not Celebes. New Guinea possesses only six species of the pantropical genus *Pheropsophus*, one occurring also in Australia and the others endemic and comprising at least one Oriental relationship, and one species of *Brachinus*. The latter genus occurs over most of the world except Australia; species are diverse in the Oriental tropics but become fewer eastward,

the New Guinean species (perhaps confined to western New Guinea) being the easternmost.

[57] The final tribe, PSEUDOMORPHINI (Part III, p. 239, with footnote 4), consists of aberrant, small and medium-sized, winged, chiefly tree-trunk-living carabids.

New Guinea possesses representatives of two Australian genera with together seven endemic New Guinean species probably representing at least five independent Australian relationships, and one endemic species of a genus that is otherwise known only from the Oriental end of the Malay Archipelago and the Malay Peninsula.

[58] *Summary of geographic units.* The geographic units (see [31]) itemized in the preceding survey of distribution of tribes of Carabidae that are represented in New Guinea (sections [33–57]) are summarized and totaled in Table 8. The table shows that New Guinean Carabidae include 104 species that occur also in the Oriental area (including Celebes and the Philippines) plus 69 additional Oriental relationships, and 69 species that occur also in Australia (beyond Cape York) plus 51 additional Australian relationships, or a total of 173 Oriental and 120 Australian geographic units. (Occurrences of additional New Guinean forms on the Moluccas in one direction and Cape York in the other are noted in sections [62] and [63].) This is, of course, a summary of the present relationships of New Guinean Carabidae without regard to their geographic histories.

It should be emphasized again that the geographic patterns are complex, that the limits of the areas compared are arbitrary, and that the selection of units (geographic units, rather than species or genera) is arbitrary too. It will be interesting to see how changes in these arbitrary decisions change the findings summarized in Table 8.

If Celebes and the Philippines were removed from the "Oriental area," and comparison made between the Oriental Region (in a strict sense) and Australia, the totals of Table 8 would be changed in favor of Australia. On the other hand, if the rain-forested areas of North Queensland, which are botanically Malaysian and to which many of the New Guinean Carabidae that do reach Australia are confined, were removed from the "Australian" area, the change would be in favor of the Orient. However, I see no reason to go further with this juggling of boundaries. The boundaries as selected, which allow comparison of the New Guinean carabid fauna with the faunas of all the major islands to the west (excluding only the Moluccas) and of virtually the whole of Australia (excluding only the Cape York peninsula) seem to me to permit a reasonably balanced assessment of the situation.

The probable effect of increase of knowledge of the fauna of Celebes should be noted. The Carabidae of Borneo and especially of Java and the Philippines and also those of New Guinea and Australia are now fairly well known, but those of Celebes and the Moluccas are much less known. If the Carabidae of Celebes were better known, they would almost surely be found to include representatives of additional New Guinean groups, which would increase the relative strength of the "Oriental" relationships of the New Guinean fauna as summarized in Table 8.

The effect of using different taxonomic units to quantify faunal relationships is more difficult to assess. If all species of Carabidae on New Guinea were counted as separate units, and if (where details are unknown) species were scored according to their general relationships, most of the 160 species of Agonini on the island would count as Oriental units, and so would most species of Harpalini of subtribes Harpalina and Acupalpina and also most Lebiini except *Demetrida*, while most of the species of Harpalini of subtribes Anisodactylina and Pelmatellina and also the 59 species of *Demetrida*, eight species of *Scopodes*, and most Licinini and Helluonini

would count as Australian. I think it is better not to attempt to make more exact counts of species which would (I think) conceal ignorance of details rather than add to knowledge of faunal relationships. It is enough to say that counting all species as separate units would not decrease but would probably increase the relative strength of the Oriental relationships of the New Guinean carabid fauna.

[59] *Geographic units by major habitats.* Table 8 can be broken down by major habitats, to see whether Carabidae in different habitats in New Guinea have different geographic relationships. I shall do this only in a general way (because too many details are unknown to allow quantification) and only for groups that occur in the lowlands (because Carabidae may change habitats as they move to higher altitudes). Among the terrestrial (mesophile) lowland Carabidae of New Guinea, those in rain forest, including various Agonini, *Perigona*, Harpalini of subtribe Harpalina, and others, seem to be mostly Oriental in relationships, while those (fewer) in opener, drier areas especially in southern New Guinea, including most Harpalini of subtribe Anisodactylina, most Helluonini (if they are terrestrial) and a few others, are Australian. Among hydrophiles, *Abacetus,* the water-loving Agonini, and most *Chlaenius,* are basically Oriental, while the pterostichine genera *Platycoelus* and *Loxandrus* and its derivatives and most of the (few) Licinini are Australian. The water-loving species of *Clivina* and *Tachys* are divided, but more of the *Tachys* probably have Oriental than have Australian relationships. Among arboreal Carabidae, the arboreal Agonini and many Lebiini (*Catascopus, Miscelus, Dolichoctis,* etc.) are Oriental in relationships, while the lebiine genus *Demetrida* and the Pseudomorphini are mostly Australian (see Table 7 for summary of geographic relationships of the Lebiini). This brief statement of the geographic relationships of New Guinean Carabidae by major habitats omits a number of small groups and groups of which the habitats or relationships are undetermined. Also omitted are important groups that have radiated primarily on New Guinea (see [91]). However, what has been said does justify the following tentative conclusions. Among lowland, ground-living (mesophile) Carabidae on New Guinea, those in rain forest are predominantly Oriental; those in opener country, more Australian. Among the hydrophiles, relationships are partly Oriental and partly Australian, but the Oriental relationships probably are more numerous. And among the arboreal forms, which occur principally in rain forest, relationships are much more Oriental than Australian, if the comparison is made in terms of geographic units. (But if the 59 species of *Demetrida* were counted as 59 Australian units, then Australian would outweigh Oriental relationships among the arboreal forms.)

To return to Table 8, the totals there given are approximations and would be changed to some extent if arbitrary decisions about the limits of areas and about the units to be counted were changed. However, on any reasonable basis of comparison, the carabid fauna of New Guinea is more Oriental than Australian, the proportion of Oriental to Australian relationships being, very roughly, as three to two. This is probably true of all the principal ecologic segments of the fauna except of terrestrial mesophiles in the opener, drier part of southern New Guinea, where Australian elements predominate. However, it should be remembered that this is an oversimplified summary of an excessively complex situation, and that although the Australian relationships of the New Guinean carabid fauna as a whole are less numerous than the Oriental relationships, nevertheless some of the Australian relationships involve important fractions of the fauna. It should be remembered too that this is a summary of *existing* relationships, without regard to origins and directions of

movement, which will be considered separately.

[60] *Transition of carabid faunas from Asia to Australia.* Ideally, the transition of carabid faunas across the Malay Archipelago should be described in terms of actual counts of genera and species as they drop out, appear, or change from island to island, but this is not yet possible. The details of distribution of many species are still too little known; the faunas of Celebes and the Moluccas are too little known; and too many genera need taxonomic revision. To obtain for Carabidae the kind of information that is now available for birds (Mayr, 1944) would require, I think, at least a lifetime of work by a competent specialist. The work would have to include years of collecting, then years of taxonomic study, then probably further years of collecting to fill gaps discovered during the taxonomic work, and finally years of assembling, mapping, and presenting the geographic data. The best I can do now is to make a general description of the apparent principal changes of carabid faunas from Asia to Australia, emphasizing major boundaries (if any) and major transition zones, and emphasizing that the description is provisional. It is based, of course, mainly on information given under the tribes in preceding pages (sections [32–57]).

Temperate Asia has a carabid fauna of which many of the dominant elements are confined to the temperate zone or at least are relatively unimportant in the tropics. Some tribes are primarily north temperate, and so are such dominant genera as *Carabus*, *Bembidion*, *Amara*, many subgenera of *Pterostichus*, *Harpalus*, and *Anisodactylus*.

The change from temperate to tropical Asia is very great, as far as Carabidae are concerned. Many dominant northern groups disappear or become insignificant; many tropical tribes and genera appear; and arboreal Carabidae, especially Lebiini, become relatively numerous.

Within the tropics, many genera and species of the Asiatic mainland reach adjacent islands of the Malay Archipelago, where a number of additional genera appear or become important; there are of course many minor changes from the mainland to the islands, but the transition as a whole is not striking.

[61] *Wallace's Line and Celebes.* Many carabid genera that reach Java and Borneo (and often the Philippines, too) do not occur on Celebes across Makassar Strait, which is the central part of Wallace's Line. Striking examples are the huge, flattened carabids of the genus *Mormolyce* (Mormolycini), and also the myrmecophilous Paussini, of which 27 species in eight Oriental genera have been recorded from Java but none from Celebes. The small tribes Hiletini and Siagonini also reach Wallace's Line from the Orient but do not cross it. Additional Oriental genera that reach this part of Wallace's Line but are not known to cross it are named in the survey of tribes [33–57] in the Ozaenini, Scaritini, Panagaeini, Pterostichini, Agonini, Licinini, Chlaeniini, Oodini, Harpalini, Lebiini, Hexagoniini, Zuphiini, and Brachinini. In the other direction, a few (but very few) Australian or New Guinean groups reach Celebes without crossing Makassar Strait to the Orient; they include *Loxandrus* (subaquatic Pterostichini), *Minuthodes* (tree-trunk-living Lebiini), and *Dolichoctis* of the *aculeata* group (foliage-living arboreal Lebiini). Wallace's Line, at least the central part of it (the distributions of Carabidae at the northern and southern ends of the Line are too little known to be discussed now), is evidently an important boundary for many, but not all, Carabidae. Actually, the Line is primarily the eastern boundary of the full-scale Oriental carabid fauna. East of it begins the main transition from Oriental to Australian faunas. Among Carabidae and many other insects the transition area extends from Celebes to New Guinea and includes the latter.

The fact that the Carabidae of Celebes are less well known than those of Java and Borneo presumably increases the *apparent* importance of Wallace's Line, but enough Carabidae are known from Celebes to show that important fractions of the fauna do change with passage from the Oriental Region proper to this island. Zoogeographically, Celebes is in fact an anomalous island for Carabidae, as it is for many other animals. Oriental genera of Carabidae that do cross Wallace's Line to Celebes but are not known to reach the Moluccas etc. include the fossorial hydrophile *Scarites*, the mesophile harpaline *Oxycentrus*, the foliage-arboreal lebiines *Lioptera* and *Callida*, the mesophile dryptine *Galeritula* (*Galerita*), and the helluonine *Macrocheilus*. A few Australian or New Guinean carabids that reach Celebes but are not found farther west are named in the preceding paragraph. The carabid fauna of Celebes seems as a whole to be more Oriental than Australian or New Guinean in relationships, but it is still much too poorly known for detailed analysis. (For a more general discussion of Wallace's Line see Mayr, 1944, and Darlington, 1957, and for the relation of the Line to some insect distributions, see Gressitt, 1959.)

[62] *Moluccas*. The Carabidae of the Moluccas too are poorly known. I have made a rough list of them, based on published records and on a collection made by myself on Morotai Island, but the total scarcely exceeds 100 species. This is surely a minor fraction of the total Moluccan carabid fauna. However, a few important Oriental groups of Carabidae do reach these islands but not New Guinea. They include two conspicuous genera, *Orthogonius* (tribe Orthogoniini) and *Trigonotoma* (Pterostichini), and one very distinct *Tachys* (*interpunctatus* Putzeys), the latter collected by myself on Morotai. On the other hand, Australian and New Guinean Carabidae that reach the Moluccas but are not known from Celebes include a *Tachys* of the *serra* group, the pterostichine genera *Prosopogmus* and *Platycoelus*, probably the agonine *Violagonum*, the harpaline *Diaphoromerus*, and the lebiine *Demetrida* (for the last see Darlington, 1968a). These details suggest that the Moluccas share more Carabidae with New Guinea than with Celebes. However, the Carabidae of the Moluccas are inadequately known, and different Moluccan islands probably have different carabid faunas with somewhat different geographic relationships. (I think the Moluccas may have been a bottleneck in dispersal, because of their small area. This possibility is further discussed in section [84].)

The change of Carabidae from Celebes through the Moluccas to New Guinea is considerable. It involves (for example) change among large Scaritini from an Oriental *Scarites* in Celebes to an Australian *Geoscaptus* in New Guinea, and among arboreal Lebiini from Oriental *Callida* in Celebes to Australian *Demetrida* in New Guinea. But these examples should not be overemphasized. Our relatively poor knowledge of the Carabidae of Celebes prevents an exact assessment of the change of Carabidae that surely does occur from this island to New Guinea.

[63] *Transition from New Guinea to Australia*. Within New Guinea itself there is transition from the still predominantly Oriental carabid fauna of the rain forest to the more Australian fauna of the opener country especially of southern New Guinea. This transition is most obvious among Harpalini [59]. It involves also disappearances of many arboreal rain-forest species that do not enter opener habitats. However, the Carabidae that do occur in opener habitats in southern New Guinea are so little known (much less well known than those in rain forest) that this transition cannot yet be described in much detail.

Transition of Carabidae from New Guinea to Australia is in part a continuation of the transition that begins within New Guinea, from the rain forest to the

more open country, for the open eucalyptus woodland of southern New Guinea is little more than a (depauperate) extension of the much larger areas of eucalyptus woodland of Australia. However, transition occurs also within the rain forest and is in fact striking as one proceeds from the great forests of New Guinea, to the isolated rain-forest tracts on Cape York, to the larger tracts farther south in eastern Australia. This transition has been described in more detail elsewhere (Darlington, 1961). I want now merely to summarize it, and to say something more about the pattern of distribution of New Guinean Carabidae on Cape York.

The transition of carabid faunas from the rain forests of New Guinea to those of Australia involves more than a change of particular genera and species. Two more-profound changes occur. One is a virtually complete change of flightless stocks, which are very few at low altitudes in New Guinea but which are more numerous and of wholly different origins in Australia, even on Cape York (see below). The other is a change from overwhelming dominance of Agonini in New Guinea to overwhelming dominance of Pterostichini in Australia (cf. [64], Fig. 13). And this change too occurs even in rain forest and even on Cape York. To the collector, these changes tend to be concealed by the occurrence of some New Guinean species in the Australian rain forests; entomologists familiar with the Australian insect fauna find the New Guinean species in North Queensland new and specially exciting. But actually, among Carabidae and I think among many other insects too, the New Guinean species form a minor fraction of the Australian fauna even in the northern rain forests.

The number of important lowland New Guinean Carabidae, most of them occurring in rain forest, that do *not* reach Australia is impressive. Among Cicindelinae, although the *Tricondyla* does reach Australia (mid-Cape York), Oriental *Therates* (with at least five species in New Guinea) and endemic *Caledonomorpha* (two species) do not, and the very small subarboreal species of *Cicindela* that have radiated in the rain forests of New Guinea are, I think, entirely unrepresented in those of Australia. The only New Guinean ozaenine (Oriental *Pseudozaena*) does not reach Australia. A few *Tachys* are common to New Guinea and Australia, but most New Guinean members of the genus, including the endemic *serra* group, do not reach even Cape York. The endemic trechine genus *Perileptodes* does not reach Australia. Among Pterostichini, the Oriental *Brachidius* and the endemic *Homalonesiota, Nebrioferonia,* and *Tiferonia* are absent in Australia. Among Agonini, *Arhytinus, Tarsagonum*, and *Euplenes* (all represented also in the Orient) do not reach Australia, nor do the endemic *Lithagonum* and *Iridagonum*, which are common at low altitudes in New Guinea, and only one of the many New Guinean species of *Notagonum* and no *Altagonum* reach Australia; the fact that *Notagonum dentellum*, *Violagonum violaceum*, and *Colpodes habilis* do occur in the Australian rain forest should not be allowed to obscure the fact that most New Guinean Agonini do not. Of 14 New Guinean *Perigona,* only the cosmopolitan *nigriceps* reaches Australia. *Oodes* of the *terrestris* group, which inhabit rain-forest leaf litter in New Guinea, do not reach Australia. Of Harpalini, *Trichotichnus, Harpaloxenus,* and *Lyter,* as well as *Hyphaereon,* which together form an important fraction of the carabid fauna on the ground in rain forest in New Guinea, are absent in Australia. The endemic New Guinean anaulacine *Odontomasoreus* does not reach Australia. Of Lebiini, *Synurus, Stenotelus, Pericalus, Oxyodontus, Mochtherus,* and some other Oriental genera represented in New Guinea fail to reach Australia, and foliage-living *Demetrida,* dominant in New Guinean rain forest, are very poorly represented in the rain forests of Australia. Among Odacanthini, *Dicraspeda* is primarily New Guinean, with only

brunnea well distributed in the Australian rain forest and *dubia* only on the tip of Cape York, and endemic *Dobodura* is unknown in Australia. And among Brachinini, *Brachinus* fails to reach Australia, and only one species of *Pheropsophus* does so. This is far from a complete list of carabids that occur in lowland rain forest in New Guinea but not in Australia. Those that do reach Australia represent a small fraction of the New Guinean carabid fauna, and they are in the minority also in the Australian rain forest, where a majority of the Carabidae are derived from Australian groups.

This is not the place to attempt to list all the Carabidae occurring in the different rain-forest areas in Australia. In any case such lists would be difficult to prepare. My collections from these rain forests are extensive but far from complete, and many of the species found are still unidentified and probably undescribed. However, some significant details are worth giving, and the occurrence of actual New Guinean species of Carabidae in the Australian rain forests is worth tabulating.

Even on the tip of Cape York, in the tip-of-peninsular rain forest (see map, Fig. 12), the outstanding carabid is an enormous, flightless pterostichine (*Mecynognathus*) of an Australian group, and the only other flightless carabid in this rain forest is a large *Clivina* closely related to species elsewhere in Australia. (Other flightless Australian Carabidae occur in the adjacent opener forest.) In the mid-peninsular rain forest, the flightless Carabidae are a large Australian pterostichine (*Paranurus*) and a probably undescribed (Australian) *Coptocarpus*. And in the much larger base-of-peninsular rain forests, the dominant Carabidae are almost all Australian; half a dozen flightless Australian genera are conspicuous; and some of them, including several genera of Pterostichini, have radiated in the rain forest. See again my 1961 paper for further details. In brief, while the relatively small rain forests

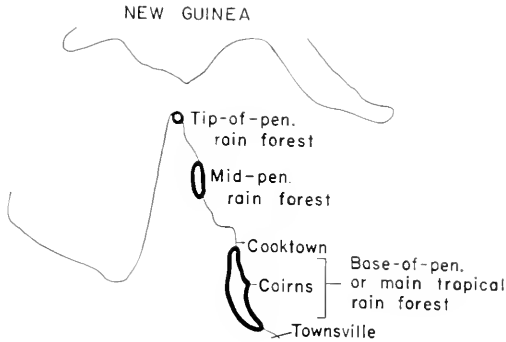

Figure 12. Distribution of rain forest in tropical North Queensland, Australia. From Darlington, 1961, p. 8, pl. 3. Heavy lines enclose principal areas of tropical rain forest, but the rain forest is usually not continuous within the boundaries shown. The rain-forested areas are separated by wide barriers of relatively dry, open eucalyptus woodland.

at the tip and middle of the Cape York Peninsula have independent, mixed (but I think more Australian than New Guinean) carabid faunas, the main tropical rain forests of Australia at the base of the peninsula are overwhelmingly Australian in their Carabidae. The situation is surely complex, and some other insects may show closer relationships between the New Guinean and Australian rain forests, but nevertheless I think it is a mistake for entomologists to include the rain forests of Australia in a Papuan region or subregion.

The distribution of rain forests in eastern Australia is mapped in Figure 12, and the known distributions of 24 New Guinean species of Carabidae in the tip-of-peninsular, mid-peninsular, and base-of-peninsular (main) rain-forest areas of tropical North Queensland are shown in Table 9. For further description of these rain forests, see my paper already cited (1961). Note that the rain-forested areas are small; actually, the rain forest is often not continuous even within the boundaries shown, but occurs in discontinuous or scattered strips or patches. The extent and continuity of rain forest in North Queensland has often been greatly exaggerated.

Table 9 is based on my own extensive

Table 9. Occurrence of New Guinean species of Carabidae in rain forest on Cape York, etc. (See Fig. 13)

Name	Tip-of-pen. forest	Mid-pen. forest	Base-of-pen. forest
Tricondyla aptera		x	
Syleter papua	x		
Clivina zebi	x	x	x
Morion longipenne	x	x	x
Caelostomus albertisi		x	
Notagonum dentellum	x	x	x
Violagonum violaceum	x		x
Colpodes habilis		x	x
Anatrichis pusilla		x	x
Coleolissus nr. *papua*	x		
Aristolebia wau	x		
Miscelus unicolor		x	
Catascopus elegans	x	x	x
" *smaragdulus*		x	
" *aruensis*		x	
Dolichoctis striata		x	
Demetrida angulata	x		
Pentagonica pallipes		x	
" *blanda*		x	x
" *erichsoni*		x	
Collinris par	x		
Clarencia quadriguttata			x
Dicraspeda brunnea	x	x	x
" *dubia*	x		

collecting on Cape York, and on previously published records. Further collecting would probably fill some gaps, but nevertheless carabid distributions evidently are irregular in these rain forests. Of the 24 New Guinean species tabulated, six have been found only on the tip of the peninsula, but only six of the other species have been found there, leaving 12 species that occur in more-southern rain-forest tracts but are apparently absent on the tip of Cape York. The tip-of-peninsular rain forest is small and of comparatively poor quality, and the carabid fauna probably really is much more limited than are the faunas of the larger and better rain forests farther south. Sixteen of the 18 species that do occur farther south have been found in the mid-peninsular rain forest. And only ten have been found in the base-of-peninsular forests (but see below).

The detailed pattern shown by Table 9 should be supplemented by two general statements. First, a few of the species tabulated, including *Violagonum violaceum*, extend still farther south in Australia. And second, a considerable number of endemic species derived from New Guinean groups exist in the base-of-peninsular rain forest, and in some cases still farther south in Australia. (This whole situation, of somewhat irregular occurrence of New Guinean species in the isolated rain forests of Cape York, and existence of additional derived species farther south, suggests continual dispersal of rain-forest species from New Guinea to Australia. The insects probably disperse with difficulty from forest tract to forest tract. Some species probably survive only temporarily in some tracts. Survival is probably correlated with area: extinctions probably occur most often in the smallest tract, which is the tip-of-peninsular one; while survival time in the largest tract, at the base of the peninsula, has often been long

enough for differentiation of species. All this is consistent with a history of continuing dispersal from New Guinea into Australia, across ecologic filter-barriers, even when there was a broad land connection. Such dispersal across ecologic barriers to a series of islands of rain forest is comparable to dispersal across water gaps to the islands of an archipelago and should be susceptible to analysis by methods developed by MacArthur and Wilson (1967).)

To complete this general account of transition of carabid faunas in the Asiatic-Australian transect, I should add that within Australia, between the tropical rain forests of North Queensland and the south-temperate rain forests of southern Australia and Tasmania, there is not only an almost complete change of species and genera but also a second partial change of dominant tribes, from Pterostichini as principal dominant mesophiles to (in the far south) dominance shared by Broscini, Trechini, Licinini, and even "antarctic" Migadopini and Merizodini, as well as some Pterostichini. This change too is described in more detail in my 1961 paper.

[64] *Summary of transitions.* In summary of transitions of carabid faunas from north-temperate Asia to south-temperate Australia, there is first a profound change of dominant tribes and genera from the north-temperate zone to the tropics in Asia; then a major transition of tropical faunas from the Orient to Australia, with the most obvious changes at Wallace's Line, between Celebes and New Guinea, and (even in rain forest) between New Guinea and tropical Australia; and finally another profound change of dominant tribes and genera from tropical to south-temperate Australia. The carabid faunas in the north and south temperate zones, at opposite ends of this series of transitions, are remarkably similar in certain ways, for example, in presence of Broscini, of flightless "*Trechus*," and of *Bembidion*. These groups must somehow have crossed the tropics in the past. However, they do not occur in New Guinea now, and further consideration of them would be out of place here. I have discussed them in more detail elsewhere (1965).

The gross changes in taxonomic composition of carabid faunas within the tropics, from Java to New Guinea to tropical Australia (North Queensland), are shown by histograms in Figure 13.[1] The histogram of the Javan fauna is based on a list extracted from my MS list of Indo-Australian Carabidae [4]. That for the New Guinean fauna is, of course, based on counts of species listed on my data sheets [16]. And that for the tropical Australian (North Queensland) fauna is based on a list extracted from my manuscript list of Australian Carabidae [4]. Many species described from "Queensland" are not known from more exact localities and may not be tropical, but on the other hand I have a number of tropical Queensland spe-

[1] The carabid faunas of Celebes and the Moluccas are too little known to be included in this comparison. Celebes is about half again larger than Java, but only about one-third as many Carabidae (only about 150 species) have been recorded from it. (Professor E. O. Wilson calculates, using data provided by me, that if Celebes were as well collected as Java and New Guinea, about 509 species of Carabidae should be known from the island.) The Moluccas are much smaller, but the number of species that occur there is presumably increased by differentiation of species on different islands of the group. About 100 species of Carabidae have actually been found there (including both those recorded in print and those found by myself on Morotai Island), but this is probably a minor fraction of the whole Moluccan carabid fauna. The following table shows the numbers of species in four principal tribes of Carabidae actually known from Celebes and the Moluccas. The figures suggest that Agonini and Lebiini are the dominant tribes on these islands as they are on New Guinea, but the figures should be considered preliminary indications only.

	Celebes	Moluccas
Pterostichini	8	13
Agonini	23	18
Harpalini	20	8
Lebiini	36	35

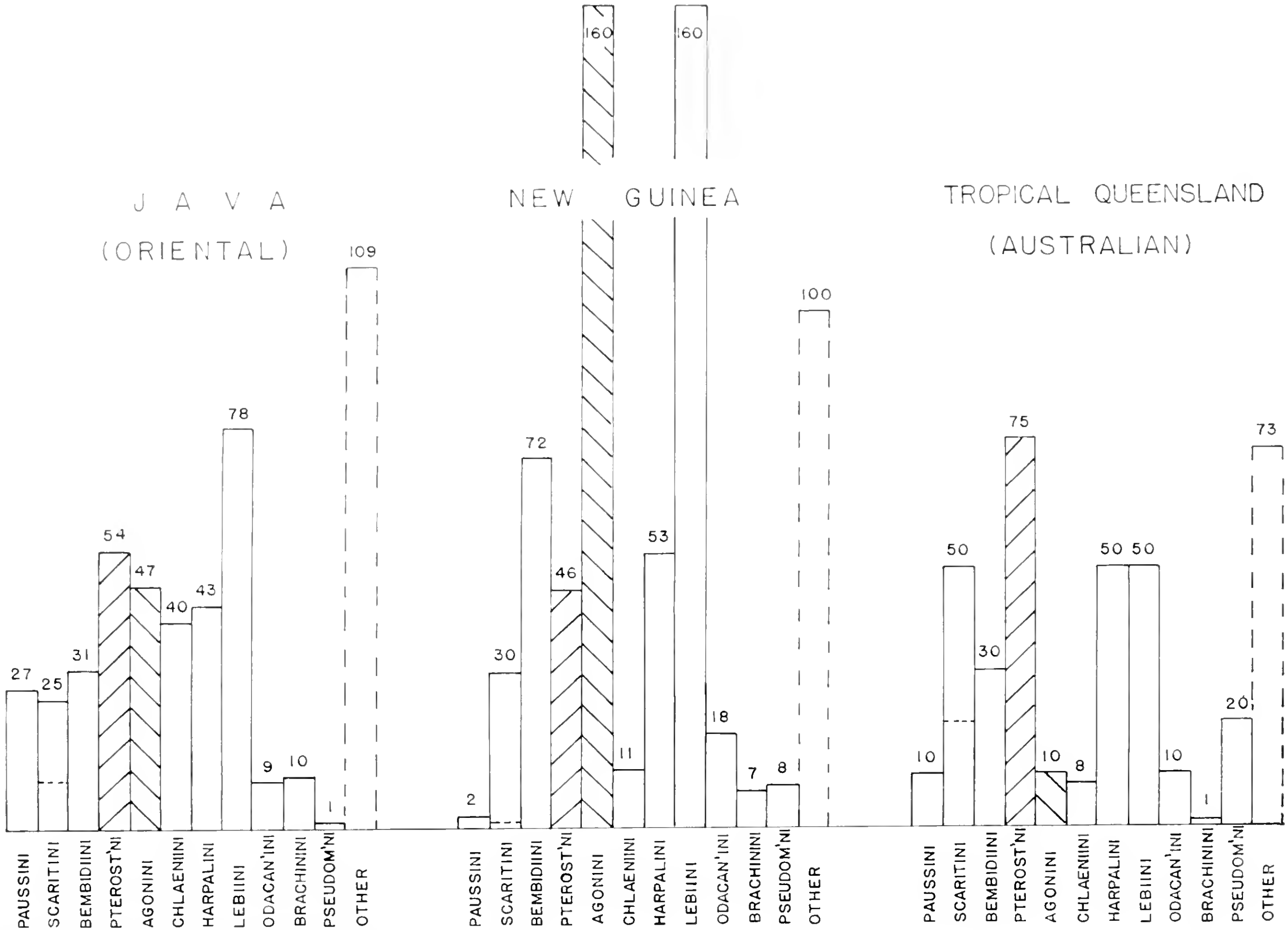

Figure 13. Histograms of the taxonomic composition of the carabid faunas of Java, New Guinea, and tropical Queensland, Australia. The columns represent numbers of species known from the areas in question in the tribes named below the columns; the actual numbers of species are given above the columns. Abbreviations are Pterost(ichi)ni, Odacan(th)ini, and Pseudom(orphi)ni. The tribes Pterostichini and Agonini are hatched to emphasize the dramatic changes in their representations in the three faunas. The columns of Scaritini are divided, the portions below the broken lines representing large, and above the lines, small forms.

cies which are undetermined and probably undescribed. I have tried to take these factors into account in totaling the North Queensland list, which is therefore based partly on estimates rather than on counts, although the estimates are carefully made, by scanning lists of species. However, I have made actual counts of species of North Queensland Agonini and in most genera of Pterostichini, so that the figures given for these two specially significant tribes are exact or nearly so.

Java is a recent continental island and its fauna is a fair if probably depauperate sample of the fauna of eastern tropical Asia, and the fauna of North Queensland is a good sample of that of tropical Australia. The three histograms therefore show major changes in composition of tropical carabid faunas from Asia to Australia. The changes that occur in several dominant tribes are worth further discussion.

The tribe Scaritini, which is the principal tribe of fossorial Carabidae, is well represented in all three faunas. However, *large* scaritines are relatively numerous in Java and (different genera) in North Queensland but very deficient in New Guinea, where almost all members of the tribe are small. The predominance of small forms in New Guinea probably reflects their greater dispersability.

Bembidiini, mainly *Tachys*, are well represented in all three faunas and include most of the very small Carabidae in all three. Many are hydrophiles, some mesophiles, and a few arboreal. The large number of these small carabids in New Guinea surely reflects their greater dispersability. They have reached the island in such numbers as to impose a second mode on the size distribution of Carabidae there (cf. [20], Fig. 8).

Harpalini and Lebiini are well represented in all three faunas. The Harpalini include many medium-sized mesophiles and a number of smaller hydrophiles. The Lebiini are mostly arboreal. Members of both tribes are evidently good dispersers. The relatively smaller number of Lebiini in North Queensland probably reflects the smaller extent of rain forest there.

Finally (as far as dominant tribes are concerned) the Pterostichini and Agonini show remarkable geographic changes of dominance. On Java, the two tribes are about equally represented. On New Guinea, Agonini are overwhelmingly dominant, being three or four times as numerous in species as Pterostichini are. But in Australia, even in the tropics, dominance is reversed, Pterostichini being many times more numerous in species than Agonini.

I have discussed this reversal of dominance before (1956; 1961), saying (1961: 22–23) "Pterostichini and Agonini tend, as dominant tribes, to be complementary over the world as a whole. . . . Both tribes are cosmopolitan, but unevenly so. In some parts of the world they occur in nearly equal numbers; in others, one tribe or the other is overwhelmingly dominant. The tribes tend to be complementary within the Australian Region, ... In [the whole of] Australia . . . (with Tasmania) Pterostichini are dominant, with more than 350 known species against probably less than 20 species of Agonini, a ratio of nearly 20/1. But in New Guinea Agonini are dominant, with considerably more than 100 known full species . . . against about 40 species of Pterostichini . . . a *reversed* ratio of about 3/1.

"One reason for the number of Agonini in New Guinea is that species of this tribe have multiplied on the mountains there. In Australia, however, Pterostichini, not Agonini, have multiplied in what seem to be comparable habitats on the mountains. This difference can hardly be accounted for in simple ecological terms but is probably due to a complex combination of ecological, historical, and geographical factors. Over the world as a whole, there is a tendency for Agonini to be better represented in the tropics; Pterostichini, in the temperate zones. Also it is probable

that Agonini, which are phylogenetically less diverse, are more recent in origin than Pterostichini and that they have dispersed more recently. It is therefore likely that Pterostichini are dominant in Australia partly because Australia is more temperate than tropical in climate and partly because Pterostichini reached Australia before Agonini did, and it is likely that Agonini are dominant in New Guinea partly because the climate there is fully tropical and partly because the carabid fauna of New Guinea is more recent in its origins than that of Australia, as I think it is. Add to this that the mountain carabid faunas of Australia and New Guinea have been derived independently, each from the lowland fauna adjacent to it, and not by dispersal along a connecting mountain chain, and we have an adequate and probably correct explanation of the great difference in composition of the carabid faunas on the mountains of Australia and New Guinea."

To extend the comparison to Java, where numbers of species of Pterostichini and Agonini are nearly equal, I suppose the Javan carabid fauna is continental in composition and includes more relatively old forms than the New Guinean fauna does, the ratio of Pterostichini to Agonini on Java being perhaps near the average for the world as a whole. The increase in relative numbers of Agonini from Java to New Guinea probably reflects the greater dispersability of Agonini as well as the lesser age of the New Guinean fauna.

[65] *Faunal regions.* The preceding summary leads to the question, in what faunal region should New Guinea be placed (if it must be placed in a faunal region), according to its Carabidae? The answer is that *if* it must be placed in a faunal region, and if the faunal regions are based (as they should be) on present geographic relationships without regard to past movements, New Guinea must be considered part of the Oriental Region, so far as its Carabidae are concerned. However, the preponderance of Oriental over Australian relationships is not overwhelming, and I prefer to take Wallace's Line as the eastern boundary of the Oriental Region and to consider the Carabidae as forming a broad transition from there to and including New Guinea. The latter can then be considered part of a transition zone, an extended "Wallacea." Or, better, New Guinea can be kept where Wallace put it (and where the distributions of vertebrates put it) as part of the Australian Region, with the understanding that the transition of Carabidae (and of many other insects) does include New Guinea nevertheless. This solution of the problem has the advantage that it does not make confusing changes in the boundaries of the conventional regions. The pattern of faunal regions is a standard known to all zoogeographers and continually referred to in describing and comparing the distributions of different groups of animals. The pattern would lose much of its value if it were continually changed to make it fit the distributions of special groups. (For more detailed discussion of the nature and usefulness of faunal regions see Darlington, 1957: 419ff.) Actually, I do not think regional boundaries are worth arguing about. What is important in any given case is to make the situation clear. The transition of carabid faunas from Asia to New Guinea and Australia is complex beyond my power of describing it in full, but I hope I have said enough to make the general outlines of it clear.

Some other families of insects in New Guinea probably show a higher proportion of Oriental relationships. This is likely to be the case among insects that are arboreal and live in rain forest. They include the Cerambycidae and Chrysomelidae studied by Gressitt, who finds that the New Guinean faunas of these beetles are more Oriental than Australian in relationships, and who therefore puts New Guinea in the Oriental Region (Gressitt, 1961, with map on p. 18). I have already given rea-

Table 10. Widely distributed oriental species or species groups of Carabidae which reach only the western part of New Guinea or (below the broken line) western and central but not eastern New Guinea, so far as known

Perileptus japonicus (Part I, p. 489), reaches the Vogelkop

Abacetus convexiusculus (Part I, p. 521), reaches Salawati I. and perhaps Dor(e)y on the Vogelkop

Anaulacus siamensis (Part III, p. 77) reaches Geelvink Bay, West N. G. (but is an inconspicuous carabid possibly overlooked farther east)

Platymetopus laticeps (Part III, p. 48), reaches the Vogelkop and Biak I.

Catascopus facialis (Part III, p. 103), is recorded from Dor(e)y (a locality always somewhat doubtful) and from Maffin Bay but has not been found farther east in New Guinea although common on many islands west of New Guinea, including Morotai I. in the Moluccas

Microlestes curtatus (Part III, p. 136), reaches Dor(e)y on the Vogelkop, if Wallace's labels are correct in this case

- -

Tachys coracinus (Part I, p. 481; present part, *Tax. suppl.*) reaches Astrolabe Bay, N-E N. G., but perhaps not extreme eastern New Guinea.

Chlaenius pan (Part III, p. 23), member of an Oriental species group, reaches Sepik District, N-E N. G., but perhaps not farther east (a conspicuous carab, not easily overlooked)

Brachinus papua (Part III, p. 239), member of an Oriental species group, reaches vicinity of Hollandia, West N. G. (also conspicuous, not easily overlooked)

sons (preceding paragraph) why the conventional faunal regions should be accepted by all zoogeographers. If entomologists must change regional boundaries, I think the changes should await aquisition of more information. The ground-living and soil-inhabiting insects of New Guinea may *not* be Oriental in their relationships, or at least not decisively so; most of them are in fact too poorly known for analysis. Surely if a system of faunal regions is to be based on the distribution of insects, it should be based on a synthesis of the distributions of many different groups and not on a few selected families. In any case I think that the insects of the main (base-of-peninsular) rain forests of Australia will prove to be more Australian than New Guinean in present relationships and probably also in origins.

[66] *Geographic patterns within New Guinea.* The distributions of Carabidae within the limits of New Guinea form a number of different geographic patterns at low altitudes, as well as a pattern of diminution and increasing geographic differentiation with increasing altitude (cf. [26, 90]). The patterns are real and significant, although probably still incompletely known in most cases.

One set of patterns is formed by species or species groups which are widely distributed outside the island but which are restricted in New Guinea itself. Several Oriental species or species groups which extend to New Guinea have been found only in the western part of the island (Table 10). Additional Oriental species and species groups will probably be found to have this pattern, of occurrence in the western but not in the eastern part of New Guinea, when the Carabidae of western New Guinea are better known; the western end of the island has been much less well collected than the eastern end. (This pattern, of course, suggests that the species that have reached only western New Guinea have arrived more or less recently from the Orient, or at least from the west. That so few recent arrivals are still restricted to the western part of New Guinea may be because most Oriental species, if they have sufficient dominance and dispersal power to reach the island at all,

TABLE 11. AUSTRALIAN SPECIES AND SPECIES GROUPS OF CARABIDAE (INCLUDING CICINDELINAE IN PARENTHESES) THAT REACH ONLY SOUTHERN NEW GUINEA OR (BELOW THE LINE) EASTERN BUT NOT WESTERN NEW GUINEA, SO FAR AS KNOWN

(*Megacephala* (Part I, p. 335), 2 Australian species recorded from Merauke, but the record may be doubtful)

(*Distipsidera* (Part I, p. 337), an Australian genus with 2 endemic species described from southern New Guinea)

[*Arthropterus novellus* (Part I, p. 354), locality within the island not specified but presumably southern New Guinea]

Clivina ferruginea (Part I, p. 387), Port Moresby

Tachys bembidiiformis (Part I, p. 464), Port Moresby (occurs also on Java, Sumba, Tanimbar, etc.; may have dispersed via the Lesser Sunda Is. and reaches New Guinea from Australia)

Tachys convexus (present part, *Tax. suppl.*), Oriomo R.

Dicrochile gigas (present part, *Tax. suppl.*), Rouku

Gnathaphanus picipes (Part III, p. 42), Port Moresby & vic., Brown R.

Gnathaphanus pulcher (Part III, p. 42), Port Moresby & vic., Bisianumu

Acupalpus brunnicolor (Part III, p. 74), Port Moresby, Oriomo R.

Lebia melanonota (present part, *Tax suppl.*), Rouku (occurs also on Java, Lesser Sunda Is., etc., but presumably reached southern New Guinea from Australia)

Basisticus micans (Part III, p. 208), Rouku

Drypta mastersi (Part III, p. 217), Rouku

Zuphium thouzeti (Part III, p. 219), Port Moresby

Helluosoma atrum (Part III, p. 233), Port Moresby & vic., Bisianumu, Rouku

Helluodema unicolor (Part III, p. 233), Rouku, Merauke

Gigadema maxillare (Part III, p. 234) Rouku

- -

Geoscaptus cacus (Part I, p. 356; present part, *Tax. suppl.*), west to vic. Hollandia

Clivina basalis (Part I, p. 383; present part, *Tax. suppl.*), west to N-E N. G. (occurs also on Celebes and Java, but N. G. specimens from Fly R. probably derived from Australia)

Clivina sellata (Part I, p. 387), at Dobodura

Craspedophorus (present part, *Tax. suppl.*), genus with numerous species in Australia and 1 endemic at Tapini, Papua (a separate group of species in the Orient)

Gnathaphanus philippensis (Part III, p. 42), Rouku and Kokoda (occurs also in Orient, but distribution in New Guinea suggests arrival from Australia)

Gnathaphanus licinoides (Part III, p. 41), west to vic. Hollandia

Hypharpax dentipes (Part III, p. 44), west to Lae and Wau (occurs also in Java, but distribution in New Guinea suggests derivation from Australia)

Lachnoderma foveolatum (Part III, p. 89), not found west of Papua

Nototarus (Part III, p. 185), an Australian genus with 1 endemic species in eastern New Guinea, at Dobodura

Parascopodes cyaneus (Part III, p. 196), not found west of Papua

Casnoidea puncticollis (Part III, p. 207), Fly R.

Pseudomorphini (Part III, p. 239), New Guinean species of *Adelotopus* and *Sphallomorpha* are endemic but apparently related to Australian species and have been found only in Papua and N-E N. G.

TABLE 12. LOWLAND CARABIDAE IN WHICH DIFFERENTATION OF SUBSPECIES OR SPECIES PAIRS HAS OCCURRED IN DIFFERENT PARTS OF NEW GUINEA

Clivina deälata (Part I, 372): a winged population on the Fly R. and different short-winged subspecies in N Papua and N central New Guinea

Clivina erugatella (Part I, 380): fully winged populations at Hollandia and Maffin Bay in West N. G., and a dimorphic population (mostly short-winged) at Aitape in N-E N. G. (although these populations are incipiently differentiated, I have not recognized them as subspecies)

Tachys serra (Part I, 405): subspecies in Papua, N central N. G., and the Vogelkop

Tachys serrula (Part I, 408): a fully winged subspecies in N-E N. G. (and New Britain), a short-winged population in N Papua

Tachys sublobatus (Part I, 418): a subspecies at Lae and Dobodura, another at Maffin Bay

Tachys mastersi (Part I, 420): a subspecies on the Vogelkop and another in the main part of New Guinea (and other subspecies or closely related species in Australia and the Philippines)

Tachys masculus (Part I, 422): subspecies in N central N. G., and the Vogelkop

Tachys pictus (Part I, 447): subspecies in Papua, N N-E N. G., and Hollandia area, (and on the Bismarck Rge.)

Tachys latissimus (Part I, 474): a subspecies widely distributed in the Oriental Region and occurring also in E New Guinea, and a melanic subspecies in N West N. G.

Abacetus haplosternus and *strancoi* (Part I, 518): a common intermediate form is widely distributed in the main part of N. G. but splits into 2 closely related species in Papua (and New Britain)

Notagonum aitape (Part II, 141): subspecies in N central N. G., and the Vogelkop

Notagonum subpunctum (Part II, 146): a subspecies in Papua, and another in the main part of New Guinea and the Vogelkop

Notagonum paludum (Part II, 150): a subspecies in Papua, and another in N N-E N. G.

Lithagonum annulicorne (Part II, 176): a distinct subspecies in Papua, less distinct ones in N N-E N. G., West N. G., (and in the mountains)

Altagonum vallicola (Part II, 190): subspecies in Papua, Huon Peninsula, and West N. G.

Altagonum grossulum (Part II, 191): a subspecies in Papua, and 2 more subspecies in different parts of West N. G. (the western subspecies are in low mountains but probably range to the lowlands too, as the Papuan one does)

Odontomasoreus humeralis (Part III, 76): a subspecies at Dobodura (Papua) and another in N central N. G.

Minuthodes sexualis (Part III, 98): a subspecies in Papua, another widely distributed in the west of N. G.

Dolichoctis divisa and *huon* (Part III, 131): a pair of apparently closely related species occurring in Papua and N N-E N. G. respectively

Anomotarus ornatus and *fuscipes* (Part III, 190): *ornatus* occurs in the Moluccas and the western part of New Guinea east of Hollandia, *fuscipes*, in eastern New Guinea west to Hollandia. A species pair, which I should call subspecies expect that they overlap in Hollandia.

have quickly spread through the whole length of it, and often to the corner of Australia, too. That the Moluccas tend to be a bottleneck in dispersal, and that the Carabidae that reach New Guinea across them tend to be relatively dominant, is suggested elsewhere [84].)

Another set of geographic patterns is formed by Australian species which reach only the southern edge of New Guinea, some of them perhaps only open eucalyptus woodland and other "Australian" habitats, or which, although somewhat more widely distributed, reach only the eastern part of the island. These species are listed in Table 11. Besides the actual Australian

species that occur in southern or eastern New Guinea, several Australian genera have endemic species apparently confined to these parts of New Guinea (see also Table 11). (This pattern, of course, suggests that the species in question, or their immediate ancestors, have reached New Guinea more or less recently from Australia, some of them over the land connection that existed at times in the Pleistocene [17].)

Still other sets of geographic patterns are formed by localization and differentiation of Carabidae at low altitudes in different parts of New Guinea. Because collecting of Carabidae has been both inadequate and uneven, geographic patterns cannot yet be fully defined for most species. However, in 20 cases (listed in Table 12) lowland Carabidae have formed subspecies or species pairs in different parts of the island. In four cases subspecies occur in the Vogelkop, with different subspecies at one or more localities elsewhere in New Guinea. In 13 cases subspecies occur in Papua, with different subspecies elsewhere in New Guinea. And in seven cases divisions between subspecies or species pairs are somewhere in the middle part of the island. (The sum of these cases is greater than the number of species and species groups listed in Table 12 because several species have divided into more than two subspecies.) It should be emphasized that even these cases are still incompletely known. That relatively few subspecies have been distinguished on the Vogelkop may be because relatively little collecting has been done there. Allowing for this inequality of collecting, I cannot see that subspecies have tended to form in significantly greater numbers in any one part of New Guinea than in other parts. The geographic patterns of subspeciation are more complex in some cases than Table 12 shows. Also, it should be emphasized that many species of Carabidae are apparently distributed over most or all of New Guinea (in appropriate habitats, of course) without obvious local differentiation.

Because different lowland areas have been unequally collected, I see no use listing endemic species known from different parts of New Guinea. Every part of New Guinea seems to have at least a few localized species of its own, in spite of the fact that many other species, probably a great majority of the lowland ones, are widely distributed on the island. However, a table of the distributions of endemic genera may be more significant (Table 13). (The table includes a few genera that are not strictly endemic but have been found to occur also in limited areas outside New Guinea.) This table shows a concentration of endemic genera mainly in the mountains and (at lower altitudes) toward the eastern end of the island. Of ten genera endemic to New Guinea and represented in the lowlands, only two are known to reach the Vogelkop and none is peculiar to the Vogelkop. It remains to be seen whether this apparent situation is real, or whether it is a reflection of the relatively small amount of collecting that has been done at the western end of the island. (It *might* be due to continual invasions of western New Guinea by new Oriental stocks and a resulting tendency of older endemic stocks to survive toward the eastern end of the island.)

In summary of geographic patterns of Carabidae at low altitudes within New Guinea, it can be said that some species and species groups that are widely distributed outside the island reach only the western or only the southern or eastern parts of New Guinea (suggesting more or less recent arrivals from the Oriental area or from Australia). Differentiation and localization of species and even of some genera in different parts of New Guinea form other patterns. Endemic genera and species may be concentrated toward the eastern end of the island, but otherwise no special centers of speciation and no specially important barriers to dispersal at

Table 13. Distributions, relationships, and ecology of "endemic" (see text) genera

(Cicindelinae)

Caledonomorpha (Part I, p. 336): 2 species confined to eastern New Guinea ("the bird's tail"), relationships probably Australian; terrestrial or subarboreal

(Carabidae proper, other than Agonini)

Perileptodes (Part I, p. 489): 2 species, 1 or both distributed throughout New Guinea including the Vogelkop (and 1 reaching the Solomons); relationships with (primarily Oriental) *Perileptus*; hydrophiles, by streams

Rhytiferonia (Part I, p. 533): 2 species, both at high altitudes on the Snow Mts.; relationships probably Australian; probably mesophiles

Analoma (*Paraloma*) (Part I, p. 538; present part, *Tax. suppl.*): 4 species, at high altitudes only; relationships probably Oriental; probably mesophiles

Haploferonia (Part I, p. 547): 1 species, known from 1 specimen from 750 m, West N. G.; relationships probably with (Australian) *Loxandrus*; probably mesophile

Homalonesiota (present part, *Tax. suppl.*): 2 species, of which 1 presumably from lowlands *c.* 80 km west of Hollandia, the other widely distributed at moderate altitudes; relationships probably with (Australian) *Loxandrus*; probably hydrophiles, by streams

Nebrioferonia (present part, *Tax. suppl.*): 1 species, widely distributed, but not yet known on the Vogelkop; relationships with preceding; hydrophile, by streams

Tiferonia (Part I, p. 563): 1 species, eastern New Guinea west to Hollandia; relationships doubtful (an apparent relative in the Philippines); hydrophile, swamps

Lyter (Part III, p. 63): 1 species, widely distributed in New Guinea; relationships probably with (Oriental) *Trichotichnus*; mesophile

Odontomasoreus (Part III, p. 76): 1 species (2 subspecies), in eastern half of New Guinea; relationships probably Oriental; mesophile

Minuphloeus (Part III, p. 117): 1 species, widely distributed at moderate altitudes; relationships undetermined; ecology unrecorded (perhaps arboreal, on tree trunks)

Dobodura (Part III, p. 215): 1 species, widely distributed at low altitudes; relationships probably with (Australian) *Eudalia*; hydrophile, by streams

Helluopapua (Part III, p. 232; present part, *Tax. suppl.*): 2 species, at moderate altitudes in West N. G.; relationships with (Australian) *Helluonidius;* probably mesophiles (possibly on tree trunks)

(Agonini, probably not derived from *Notagonum/Colpodes* ancestors)

Tarsagonum (Part II, p. 127; present part, *Tax. suppl.*): 1 species, Papua and N-E N. G. (and a species from Borneo has now been assigned to this genus); relationships Oriental; mesophile

Idiagonum (Part II, p. 229; present part, *Tax. suppl.*): 6 species, at high altitudes on several mountain ranges; relationships Oriental (probably derived independently of other New Guinean agonines); mesophiles

(Agonini, probably derived on New Guinea from *Notagonum/Colpodes* ancestors)

Lithagonum (Part II, p. 176): 1 species (several subspecies), probably throughout New Guinea but not yet actually recorded from the Vogelkop; probably related to other New Guinean agonines (which originally derived from Orient); hydrophile, by streams

Iridagonum (Part II, p. 181; present part, *Tax. suppl.*): 7 species, at low and moderate altitudes throughout New Guinea including the Vogelkop; probably related to other New Guinean agonines (which originally from Oriental stock); mesophiles

Eight other apparently endemic agonine genera (Part II; present part, *Tax. suppl.*): total of 59 species all confined to the mountains; all probably derived from the (nonendemic) "genera of convenience" *Notagonum, Colpodes,* and *Altagonum* (which have diversified on New Guinea, but which are all probably derived from Oriental stocks); mostly mesophiles, but *Potamagonum* and some species of *Nebriagonum* hydrophiles, by streams, and 1 *Nebriagonum* and perhaps some species of other genera (especially *Maculagonum*?) subarboreal

low altitudes within the island are indicated. (Apparently many lowland Carabidae have dispersed freely within the limits of the island. Their dispersals and later differentiations have formed a number of different patterns, but no one pattern is uniquely important. Rather, all the dispersals and differentiations together have formed a complex network of geographic patterns over the lowlands of New Guinea as a whole, and the network is *not* divided into major parts by well-defined barriers.)

At higher altitudes, every principal mountain range has been a center of differentiation of species and sometimes of genera, and deep valleys between high ranges have been important barriers. This is surely true. However, so little collecting has been done at high altitudes, and collecting on different mountain ranges has been so unequal, that patterns of distribution of Carabidae at high altitudes cannot yet be usefully discussed.

ZOOGEOGRAPHY: DISPERSALS AND GEOGRAPHIC ORIGINS

I shall now turn from description of existing geographic patterns to consideration of the movements—dispersals—that have made the patterns. Existing patterns are complex enough and difficult enough to describe fairly (see [31]), and the movements that have made the patterns are even more complex and difficult to reconstruct without prejudice. I suppose that all writers on this subject do have prejudices. One of mine is, in the absence of conclusive evidence, to prefer dispersals from large to small areas, in this case from Asia to Australia, rather than the reverse. Having acknowledged this prejudice, I shall try to guard against it.

[67] *The apparent main pattern of dispersal.* All faunas are derived, geographically. Nowhere in the world is there an existing fauna that cannot be accounted for in terms of derivations from other parts, if one goes far enough back in evolutionary and geographic history. Animals have in fact formed a continually changing pattern —a zoogeographic kaleidoscope—of evolutions, dispersals, retreats, and extinctions, proceeding in many different directions over the world as a whole. Every part of the world is continually invaded or liable to invasion by animals from other parts, and every part of the world has some chance of originating groups that disperse to other parts. The details are almost inconceivably complex. Nevertheless, I think the kaleidoscope has a main pattern. Dominant groups apparently evolve most often in certain places, in the largest and most favorable areas, and most often disperse in certain directions, into smaller and less favorable areas. I have discussed this fundamental pattern several times, most thoroughly in 1959, and most recently in a careful summary in 1965, Chapter 5, on "Area, climate, number of species, evolution, and dispersal." The main area of the Old World tropics seems to me to have been the greatest of all evolution-dispersal centers, from which successive dominant stocks have spread over the world. Australia has been another center, although (from a worldwide point of view) much less important than the main Old-World-tropical one. Australian animals have evolved diversely, and many have dispersed to surrounding islands, but very few of them have gone far.

[68] *Dominance, competition, and extinction in dispersal; faunal overturn.* The geographic history of animals seems to me to have been primarily the history of dispersals of successive dominant groups.

Dominant animals are conspicuously successful ones. Dominant groups are relatively numerous in individuals, often numerous in species, often diverse in adaptations, and often widely and continuously distributed in more or less diverse habitats. Examples among Carabidae are (within their ecologic limits) *Clivina* among fossorial forms, *Tachys* (in the tropics) and small Harpalini among hydro-

philes, some Agonini in a variety of habitats (except very dry ones), some medium-sized Harpalini on the ground, and some Lebiini in arboreal habitats (especially in the tropics). Dominance presumably reflects underlying qualities—"general adaptations" (Darlington, 1948: 109; 1957: 565; Brown, 1958)—that make for initial success and that lead to evolution of numerous, varied, successful types.

Dominance implies success in competition, competition being defined as any interaction among organisms that is or may be disadvantageous to any of them. Although competition is difficult to demonstrate in particular cases, the general evidences of it in the animal world are overwhelming. The strongest evidence comes from the general level and balance of faunas in all parts of the world (Darlington, 1957: 552ff). For example, every habitable part of the world has a carabid fauna roughly proportional to area and climate, and the Carabidae in each part show a reasonable range of size and include representatives of all the principal ecologic groups for which habitats are available. No substantial part of the world is overfull of Carabidae, and no part has a notable deficiency of them. This balance cannot be due to chance. Something must hold the size and composition of carabid faunas everywhere within certain limits in spite of continual multiplications and dispersals of successive phylogenetic groups. Only competition can do this, and to do it competition must be a fundamental, omnipresent force, resulting in continual extinction of undominant stocks as dominant ones spread and diversify.

I have reviewed this subject here because the role of dominance and competition in spreading, recession, and extinction must be understood if the nature and history of the existing carabid fauna of New Guinea are to be understood.

[69] *Complexity of dispersal.* Dispersals must often be almost inconceivably complex. The dispersals of most tribes and of many genera are the sums of the dispersals of many species, and the dispersals of species are the sums of movements of multitudes of individuals. Moreover, extinctions (withdrawals) as well as spreadings must be important in the dispersal histories of many groups of animals. We know from their unique fossil record that mammals have had a very complex dispersal history, with successive dominant groups spreading over much or all of the world, the spread of new major groups being accompanied by localizations and extinctions of previously dominant groups. The Carabidae have left virtually no fossil record, but they are probably more diverse taxonomically, older, and (because most of them are winged) more rapid in their dispersals than the mammals are, and their geographic history may have been even more complex than the history of mammals, with more successive dispersals and more extinctions. Along any one line of dispersal, many groups of Carabidae are likely to have spread and many others to have "retreated" (become extinct in parts of their ranges), and both processes are likely to have occurred in both directions in different groups along the line of dispersal. Nevertheless net changes of distributions amounting to directional movements of whole faunas may have occurred in the course of time. We want now to find whether there has been a net direction in the movements of Carabidae in the Asiatic-Australian area, whether the direction can be detected by analysis of carabid distributions, and how New Guinean Carabidae fit into the dispersal pattern.

[70] *Place of New Guinea in the main dispersal pattern.* The vertebrates of New Guinea are mostly Australian in their closest relationships, while the Carabidae are more Oriental than Australian, but the vertebrates and carabids do share one significant characteristic: New Guinea has not been a major dispersal center for either of them. Groups that seem to have evolved

and diversified primarily on the island have usually not spread far. For example, the birds of paradise, which have diversified extraordinarily on New Guinea, are represented (in very small numbers) westward only to the Moluccas and southward only to northeastern Australia. Among mammals, murid rodents of the subfamily Hydromyinae seem to have diversified primarily on New Guinea; one genus has spread over Australia (and to New Britain) and another genus is localized in northeastern Australia, but New Guinean hydromyines do not extend westward, although a few possibly related forms are (relict?) in the Philippines.

Among Carabidae, too, very few groups have patterns of distribution that suggest evolution in and spread from New Guinea itself. No tribe of Carabidae is peculiar to or centered on the island. Of genera, the foliage-living section of *Demetrida* (Part III, pp. 140ff) does seem to have evolved or at least diversified in New Guinea, but it has dispersed (in very small numbers) westward only to the Moluccas and southward only to northern Australia; the total distribution of these insects is very much like that of the birds of paradise (above). *Minuthodes* (Part III, pp. 95ff) may be primarily New Guinean, but if so it has dispersed only as far as Celebes, New Britain, and northern Australia. *Dolichoctis* of the *aculeata* and (derived?) *polita* groups (Part III, pp. 128ff), with ten species on New Guinea, reach only to Celebes, New Britain and New Ireland, the Solomons, and northern Australia. *Dicraspeda* (Part III, pp. 210ff) has six diverse New Guinean species, one of which extends to Java and the Philippines and to northern Australia (another reaches the tip of Cape York); this is, I think, the widest dispersal of any primarily New Guinean group of Carabidae. These are the principal groups of Carabidae that are distributed as if they have originated in and spread from New Guinea. The *serra* group of *Tachys* (Part I, pp. 404ff), with three distinct species on New Guinea, and with outlying forms reaching the Moluccas and New Britain (not Australia), is an example of a smaller group distributed as if it has diversified in New Guinea and dispersed for short distances beyond the limits of the island.

Of course some Carabidae have differentiated and radiated on New Guinea (see especially [91, 92]), but the island has been much less important as an evolutionary center than the continents have been and has not been a major dispersal center for these insects. Most carabids that have reached the island have apparently come in from Asia or Australia, or have dispersed across New Guinea from one continent to the other. The question now is, what has been the net direction of dispersal of these insects between Asia, New Guinea, and Australia?

[71] *Directions of dispersal.* The sums of nondirectional geographic units at the bottom of Table 8 [58] give a ratio of 173:120 Oriental to Australian relationships for New Guinean Carabidae, and this at least suggests more movement from the Orient to New Guinea than from Australia to New Guinea. However, this situation *might* be explained in other ways, for example by movements of New Guinean stocks to the Orient or by extinctions of New Guinean stocks in Australia, and the Australian relationships of considerable numbers of New Guinean Carabidae *might* be the result of movements either from Australia to New Guinea or from New Guinea to Australia. It is therefore important to look for other evidences of direction of movement to confirm (or contradict) the generalization that Table 8 suggests.

[72] *Direction and vagility.* Correlation of relative dispersal ability with geographic relationships might give evidence of directional movement. The Bembidiini and Perigonini of New Guinea total 31 Oriental to ten Australian geographic units, and the *arboreal* Agonini and primarily arboreal

Lebiini total 35 Oriental to 16 Australian geographic units; the sums for all these groups together are 66 Oriental to 26 Australian units. If these figures are subtracted from the grand totals of 173 and 120 (Table 8), the sums of geographic units for all other New Guinean Carabidae are found to be 107 Oriental to 94 Australian. The Bembidiini (principally *Tachys*, see [20] and Fig. 8) and Perigonini (*Perigona*) include most of the very small Carabidae in New Guinea and, because of their small size, they probably disperse through the air more rapidly than larger Carabidae. And the arboreal agonines and lebiines are active and fly more readily than most other Carabidae, and they too are likely to disperse rapidly. The geographic relationships of these groups show that they have in fact made multiple dispersals in the Asiatic-Australian area. If there is a net direction in dispersal, the more rapidly dispersing groups might be expected to run ahead of the more slowly moving groups and thus to show net direction of movement, and the groups just specified do in fact show significantly more Oriental and fewer Australian relationships than other New Guinean Carabidae do, suggesting that the main direction of movement has been from the Orient toward New Guinea and Australia. This is, however, only a tentative conclusion, which depends on (among other things) the assumptions that there is a net direction of movement and that the whole situation is relatively simple, not distorted by massive extinctions.

[73] *Carabid versus mammalian dispersals.* This same method, of comparing more with less vagile groups, can be extended by comparing the patterns of distribution of Carabidae and of mammals. While the Carabidae of New Guinea are (roughly) three parts Oriental to two parts Australian in present relationships, the mammals of New Guinea are overwhelmingly Australian, excepting the bats (Darlington, 1957: 335, Table 8; Keast, 1968). Of flightless land mammals, New Guinea, like Australia, possesses only a few monotremes, many marsupials, and rodents of the family Muridae, and even the murids are (in terms of present relationships) much more Australian than Asiatic. Among these New Guinean mammals, degree of relationship with Asiatic mammals is correlated with power of dispersal: the monotremes and marsupials have no existing Asiatic relatives; the rodents, which cross water barriers more often than other terrestrial mammals (as we know from situations in many parts of the world), do show Asiatic ties, some older and some more recent; and the bats, which obviously have still greater power of crossing water barrriers, are still more Asiatic and less differentiated in New Guinea and Australia. In this case, we know beyond reasonable doubt that six or more stocks of murid rodents (Simpson, 1961) and many stocks of bats have in fact dispersed from Asia toward Australia, and the closeness of relationships of the New Guinean (and Australian) to Asiatic forms are roughly in proportion to the powers of dispersal of the different groups. This is the same pattern that has been found [72] in comparing the more with the less readily dispersed groups of New Guinean Carabidae, and the explanation is probably the same, that the carabids too have dispersed mainly from Asia toward New Guinea and Australia, the most actively dispersing groups showing their Asiatic relationships and origins most strongly.

The pattern of relationships of New Guinean Carabidae can be compared directly with the mammalian pattern. The primarily winged carabids surely disperse across barriers more easily than terrestrial mammals do. New Guinean Carabidae are much more Oriental and less Australian in their relationships than New Guinean mammals are, and I think this is evidence both that the Carabidae have dispersed more recently and that the direction of their dispersal has been mainly (but of

course not exclusively) from Asia toward New Guinea and Australia.

Another conceivable explanation of their different geographic patterns in the Asiatic-Australian area is that Carabidae are older than mammals; that existing carabids dispersed before the mammals did, while New Guinea and Australia were connected by land with Asia; and that the land connections were broken before the mammals radiated in the Australian Region. I think, however, that the facts are decisively against this possibility. I recognize 104 actual species of Carabidae common to New Guinea and the Oriental area. Further taxonomic work may show that in some of these cases the New Guinean and Oriental populations are distinguishable, but there can be no serious doubt that many species of Carabidae do now range from the Orient to New Guinea, some species even from the mainland of Asia to Australia. Granted that rates of evolution vary and that speciation may have occurred relatively slowly in some Carabidae, it is nevertheless unlikely that so many species have not only remained identical in the Orient and New Guinea but have also maintained their geographic ranges since the beginning of the Tertiary, which (as the fossil record of mammals shows) is the latest there can have been a complete land connection between Asia and the Australian Region, if there ever was a connection. I therefore think that the general pattern of relationships of different groups of Carabidae, and comparison with the pattern of distribution of mammals, does give strong indications that the carabids have dispersed relatively recently and mainly from Asia toward New Guinea and Australia.

[74] *Directions of dispersal of tribes, genera, and species.* Besides the general indications of direction derived from the nature and relationships of the fauna as a whole, from comparison of some more-vagile groups of Carabidae with less-vagile ones, and from comparison of the Carabidae with the mammals (above), more specific evidence of direction can be found in the patterns of distribution of some tribes, genera, and species of Carabidae. This evidence is of a different sort from that analyzed above and sometimes contradicts it, or rather clarifies it, for present closest relationships (considered above) show only the most recent in what may have been a complex series of dispersals. For example, the closest relationships of the rodents of New Guinea are now with Australian rodents, but the pattern of distribution of the whole family Muridae and also the fossil record show that the ancestors of New Guinean and Australian murids all came from Asia in the first place. For another example, *Chlaenius* in New Guinea now includes nine Oriental to six Australian "geographic units" of present relationships, but the pattern of distribution of the genus as a whole and also the distributions of several of the species (Part III, pp. 20ff) suggest multiple movements from Asia toward Australia. In this case the failure of some "geographic units" to show direction decisively seems to be due to the effectiveness of dispersal, for several stocks seem to have dispersed from Asia across New Guinea and into Australia, so that they count as both Oriental and Australian in terms of present distribution even though dispersal may have occurred in only one direction. On the other hand, New Guinean Licinini include four Oriental and five Australian geographic units, but the tribe is now much more Australian than Oriental in its distribution, and it seems likely that movements from Australia across New Guinea into the edge of the "Oriental area" have been relatively more important than the geographic units show.

Criteria for determining probable directions of dispersal of specific groups have been discussed by me in 1957, pages 31–35. In the absence of a significant fossil record, the best clues to directions of movement are based on relative numbers and relative areas: if a genus is represented by (say) 50 species on one continent and

one species on another, dispersal is likely to have been from the first to the second continent, and if a species occurs over the whole of one continent and only on the corner of another, dispersal is again likely to have been from the first to the second continent. But clues like these must be used judiciously. They are likely to be most trustworthy in dominant (conspicuously successful) groups, in which distributions are still continuous, and in which there are definite clines of numbers in given directions, or great inequalities in areas occupied on different continents, for these groups are most likely to have dispersed recently or to be dispersing now, so that their distribution patterns really do reflect dispersals rather than local radiations, extinctions, and other complications. Carabidae are primarily winged insects which do fly and can disperse rapidly, in spite of the fact that some have lost the power of flight. Their movements over the world and between adjacent continents have probably been very numerous and very complex. And, to judge from what has happened among other animals of which we have better fossil records (especially the mammals), the multiple and successive dispersals of dominant carabid groups have probably been accompanied by frequent and widespread extinctions of other groups. Therefore, I do not trust "numbers clues" or "area clues" to show directions of movement of nondominant, discontinuously distributed groups, of which the present distributions may be the result of withdrawals (partial extinctions) rather than of initial dispersals (cf. *Loxandrus*, [82]). (Zoogeographic tracking is like tracking in snow in that the tracker can follow with the most confidence the clearest, most recent trails rather than older, partly obliterated ones.)

With these criteria and their limitations in mind, I want now to survey the tribes of Carabidae that are represented in New Guinea and to try to pick out the groups that clearly show evidences of direction of dispersal. Evidence might come from the distributions of tribes as wholes, or of genera, or of species. In any single case, no matter how clear the evidence seems to be, the conclusions should be considered tentative. But if, of many separate cases, most seem to show dispersal in the same direction, the probability that dispersal has had a net direction will become strong. However, no matter how great the preponderance of movements in one direction, some counter-movements are to be expected too; this seems always to be the case in complex faunal movements.

The groups of Carabidae that seem to show directions of dispersal are listed in Table 14. The table is derived mostly from the preceding survey of tribes (items [33–57]). Most of the details that seem to me to indicate direction have been given in this survey (or under the groups concerned in Parts I–III and the present *Taxonomic supplement*) and will usually not be repeated here. Evidence of direction of movement may, of course, be derived not only from the distribution of a given genus or species but also from the occurrence of related forms—whether they are Oriental or Australian. The following abbreviations are used: Or, Oriental area; NG, New Guinea; Au, Australia beyond Cape York; CY Cape York; Mol, Moluccas. "Or to NG to Au" means that dispersal has apparently been from the Oriental area to New Guinea to Australia. In this table I have indicated movements from New Guinea to Cape York or from New Guinea to the Moluccas only when they are continuations of longer movements from the Orient or Australia respectively. To include other short-range movements would weight the results in favor of movements toward Australia, because the Carabidae of Cape York are better known than those of the Moluccas.

[75] *Summary of direction to this point.* The 128 groups (tribes, genera, and species) of Carabidae listed in Table 14, that seem to show relatively clear evidences of

TABLE 14. GROUPS OF NEW GUINEAN CARABIDAE THAT SEEM TO SHOW DIRECTIONS OF DISPERSAL

In tribe Ozaenini: *Pseudozaena orientalis* with subsp. *opaca*, Or to NG.

In tribe Paussini: *Arthropterus*, Au to NG.

In tribe Scaritini: *Geoscaptus cacus*, Au to NG; *Syleter*, Or to NG to CY; *Clivina zebi*, Or to NG to CY. (Other *Clivina* in New Guinea are in part Australian- and in part Oriental-related, but I think they are not well enough known to justify deductions about their directions of dispersal.)

In tribe Bembidiini: *Tachys* as whole, mostly Or to NG to Au; *T. fasciatus*, Or to NG to Au; *T. ceylanicus*, Or to NG; *T. klugi*, Or to NG; *T. convexus*, Au to NG; *T. fumicatus*, Or to NG (closely related *curticollis* may not have moved Au to NG but may represent a first invasion from Or to NG to Au of an Or stock that later reinvaded NG as *fumicatus*); *T. umbrosus*, Or to NG; *T. coracinus*, Or to NG; (some other *Tachys* have distributions that suggest dispersal either from Or to NG or from Au to NG, but the evidence seems less clear than in the cases cited); *Limnastus atricapillus*, Or to NG.

In tribe Trechini: *Perileptus*, Or to NG to Au.

In tribe Panagaeini: *Peronomerus xanthopus*, Or to NG; *Dischissus notulatus*, Or to NG; *Craspedophorus gressittorum*, Au to NG.

In tribe Pterostichini: *Morion* of Or group, Or to NG to Au; (*Mecyclothorax*, see [80]); *Brachidius crassicornis*, Or to NG; *Caelostomus* (excluding *picipes*), Or to NG to CY; *Abacetus haplosternus*, Or to NG to Au; *A. convexiusculus*, Or to NG; *Lesticus*, Or to NG to Au; *Prosopogmus*, Au to NG to Mol; *Platycoelus*, Au to NG to Mol; *Loxandrus*, Au to NG to Or (Celebes) (see [82]).

In tribe Agonini: tribe as a whole, mainly Or to NG to Au; *Euplenes*, Or to NG; *Dicranoncus queenslandicus*, Or to NG to Au; *Lorostemma*, Or to NG; *Agonum* (*Sericoda*) *ceylanicum*, Or to NG (see [80]); *Notagonum dentellum*, NG to Au; *N. submetallicum*, Au to NG; *Violagonum violaceum*, NG to Au; *Colpodes sapphyrinus* with subsp. *sloanei*, Or to NG; *C. habilis*, NG to Au; (directions of dispersal of some other Agonini are indicated, but the evidence seems less clear than in the cases cited).

In tribe Perigonini: *Perigona* as whole, Or to NG to Au; *P. plagiata*, Or to NG.

In tribe Licinini: *Badister sundaicus*, Or to NG to Au; *Physolaesthus*, Au to NG to Or (Java, Philippines); *Dichrochile*, Au to NG; (*Microferonia*, see [80]).

In tribe Chlaeniini: *Chlaenius ceylanicus*, Or to NG to Au; *C. maculiger*, NG to Au; *C. guttula*, Or to NG; *C. amplipennis*, Or to NG; *C. bimaculatus* group, Or to NG; (directions of dispersal of some other *Chlaenius* are indicated, but the evidence is less clear than in the cases cited).

In the tribe Harpalini: *Gnathaphanus* as whole, Au to NG to Or (SE Asia); *G. licinoides*, Au to NG; *G. upolensis*, Au to NG to Or (to Malay Pen.); *G. picipes*, Au to NG; *G. pulcher*, Au to NG; *Diaphoromerus*, 2 stocks, Au to NG to Mol, and Au to NG; *Hypharpax*, Au to NG to Or (Java, Sumatra); *Lecanomerus*, Au to NG; *Chydaeus*, Or to NG (see [80]); *Platymetopus*, Or to NG; *Trichotichnus*, 3 stocks, Or to NG; *Coleolisus*, Or to NG to CY; *Egadroma*, 3 stocks Or to NG to Au, and 1 stock Or to NG; *Stenolophus*, 2 stocks Or to NG to Au; *Acupalpus*, 3 stocks Or to NG to Au.

In tribe Cyclosomini: *Anaulacus siamensis*, Or to NG; *Caphora humilis*, Or to NG to CY; *Sarothrocrepis*, Au to NG to Or (Java, Philippines).

In tribe Lebiini: *Aristolebia*, Or to NG to CY; *Physodera*, Or to NG; *Lebia*, Or to NG to Au; *Holcoderus*, Or to NG to Au; *Minuthodes*, NG to Au, NG to Or (Celebes); *Catascopus* as whole, Or to NG to Au; *C. facialis*, Or to NG; *C. elegans*, Or to NG to Au; *C. smaragdulus*, Or to NG to CY; *Pericalus*, Or to NG; *Coptodera* as whole, Or to NG to Au; *C. eluta*, Or to NG; *Agonochila*, Au to NG; *Mochtherus*, Or to NG; *Dolichoctis* as whole, Or to NG to Au; *D. striata*, Or to NG to Au; *D. aculeata*, NG to Or (Celebes); *Stricklandia*, NG to Au; *Peliocypas*, Or to NG; *Syntomus*, Or to NG to Au; *Apristus*, Or to NG; (I have not counted *Anchista binotata* and *Endynomena pradieri*, both probably carried by man from Or to NG); *Demetrida*, Au to NG to Mol (but see [80]); *Phloeocarabus*, Au to NG; *Trigonothops*, Au to NG; *Nototarus*, Au to NG.

TABLE 14. Continued

In tribe Pentagonicini: *Pentagonica* as whole, Or to NG to Au; *P. pallipes*, Or to NG to CY; *P. blanda*, Or to NG to Au; *P. erichsoni*, Or to NG to CY; *P. ruficollis*, Or to NG to Au; (*Scopodes*, see p. 228).

In tribe Hexagoniini: *Hexagonia*, Or to NG to Au.

In tribe Odacanthini: *Colliuris*, Or to NG to Au; *C. fuscipennis*, Or to NG; *Clarencia*, Au to NG; *Dicraspeda*, NG to Au, NG to Or (Java, Philippines); *Lachnothorax*, Or to NG.

In tribe Dryptini: *Drypta mastersi*, Au to NG.

In tribe Zuphiini: *Planetes*, Or to NG to Au.

In tribe Helluodini: *Pogonoglossus*, NG to Au.

In tribe Helluonini: *Creagrus*, Or to NG to Au; *Helluosoma*, Au to NG; *Helluodema*, Au to NG; *Gigadema*, Au to NG.

In tribe Brachinini: *Pheropsophus*, Or to NG to Au; *Brachinus*, Or to NG.

In tribe Pseudomorphini: *Adelotopus*, 1 stock Au to NG to Or (Java) and 2 stocks Au to NG; *Sphallomorpha*, 3 stocks Au to NG; (*Cryptocephalomorpha* occurs from NG to the Malay Pen. and Thailand, but its direction of dispersal is not clear).

directions of dispersal, are classified and totaled in Table 15. The grand totals are 89 groups that seem to have dispersed southeastward, including 44 groups that seem to have spread all the way from some part of the Oriental area to some part of Australia (including Cape York), and 39 groups that seem to have dispersed northwestward, including seven groups that seem to have spread all the way from Australia to some part of the Oriental area.

It should be repeated and stressed that the groups considered to show clear evidences of directions of dispersal have, necessarily, been selected somewhat arbitrarily. The totals would vary to some extent with judgments about which groups really show direction clearly. But on any reasonable basis of selection the tribes, genera, and species that seem to have dispersed from the Oriental area to New Guinea and Australia far outnumber those that seem to have dispersed from Australia to New Guinea and the Orient. This disparity is greatest among the groups that have moved the longest distances. Many primarily Asiatic or African-Asiatic genera include species that extend eastward across the Malay Archipelago to the mainland of Australia. But very few primarily Australian groups include species that extend across the islands to the mainland of Asia; in fact *Gnathaphanus*, with one common Australian species reaching the Malay Peninsula and another reaching India etc., is the *only* carabid genus that seems to show this reverse pattern clearly. (The

TABLE 15. SUMMARY OF APPARENT DIRECTIONAL DISPERSALS OF NEW GUINEAN CARABIDAE

Or to NG	37
Or to NG to CY	9
Or to NG to Au	35
NG to Au	8
SE movements	89
Au to NG	25
Au to NG to Moluccas	4
Au to NG to Or	7
only to Celebes, 1 (*Loxandrus*)	
to Java, 1 (*Adelotopus*)	
to Java and Philippines, 2 (*Physolaesthus*, *Sarothrocrepis*)	
to Sumatra, 1 (*Hypharpax*)	
to Malay Pen., 1 (*G. upolensis*)	
to India, etc., 1 (*Gnathaphanus*)	
NG to Or	3
only to Celebes, 2 (*Minuthodes*, *Dolichoctis aculeata* group)	
to Java, 1 (*Dicraspeda*)	
NW movements	39

mainly Australian tribe Pseudomorphini reaches the southeastern corner of Asia, but the only genus that does so (*Cryptocephalomorpha*) is not Australian and its geographic history is doubtful.) This whole situation suggests not only that movements from Asia toward Australia are much more numerous than the reverse, but also that the reverse movements are usually shorter.

[76] *Direction and dominance.* Thus far, I have been considering directions of dispersal in the whole carabid fauna without distinguishing different fractions of it, except that I have compared certain relatively vagile forms (especially very small ones) with the rest of the fauna. Now, I want to compare the apparent directions of dispersal of different faunal fractions to see if the comparisons will give further information about the origins and history of New Guinean Carabidae.

Among the Carabidae of the Asiatic-Australian area, the genera *Chlaenius* (Part III, pp. 20ff) and *Egadroma* (Part III, pp. 69ff) are notably dominant. Each genus includes several species that are very widely distributed, ranging from Asia to Australia, and individuals of some of the species are numerous. The distribution patterns of these two genera have noteworthy characteristics in common. In both genera, the relative numbers and diversity of species on different continents and the relative areas occupied seem clearly to indicate origin in the main part of the Old World and multiple dispersals toward and into Australia (*Chlaenius*, into the Americas too). Some species in each genus are now widely distributed in Australia as well as in the Orient. Considered singly, these species scarcely show the directions of their dispersals, although the geographic patterns of the genera as wholes do clearly indicate direction. These and most other really dominant Carabidae, for example *Tachys fasciatus* (Part I, p. 414), seem to have dispersed from Asia to Australia. This fact is significant because the most dominant members of a fauna are most likely to have dispersed recently and to be dispersing now, and to show the main direction of dispersal of the whole fauna, if there is a main direction.

Several of the most widely distributed and commonest species of these genera, *e.g.*, *Chlaenius flaviguttatus* and *Egadroma smaragdula*, occur in a rather wide variety of wet places, although some other species of both genera have moved into drier habitats. These are examples of what I think is a fact, that ground-living carabids associated with water (hydrophiles) disperse and also cross climatic barriers more easily than most other Carabidae (see [84]).

[77] *Direction and size.* Although small Carabidae disperse more easily than large ones, *direction* of dispersal is apparently not correlated with size of insects. The very small Carabidae that have reached New Guinea have probably dispersed more rapidly than most larger ones and may show stronger Oriental relationships for this reason [72], but the larger Carabidae too (including for example *Lesticus*, *Chlaenius*, large *Colpodes*, and *Catascopus*) seem to be more Oriental than Australian in derivation. The two largest Carabidae in New Guinea are both Australian species, but one (*Catadromus tenebroides*, Part I, p. 563) is probably man-carried and is probably not established on the island, and the other (*Gigadema maxillare*, Part III, p. 234) is known from just the southern edge of New Guinea, and is a unique case and not an integral member of the New Guinean fauna.

[78] *Direction and wings.* Although winged, flying Carabidae disperse more easily than flightless ones, *direction* of dispersal is not strongly correlated with presence or absence of wings in the present case. Almost all New Guinean Carabidae, whatever the present state of their wings, are or may be derived from ancestors that were winged when they reached the island [84, 88], regardless of the direction from

which they came. The only sure exception is the flightless tiger beetle *Tricondyla,* which came from the Orient, probably by rafting (cf. [21], footnote). The three other carabids most likely to have reached New Guinea without flying are all Australian, as would be expected from the fact that New Guinea was connected with Australia not long ago [17]. They are species of *Craspedophorus* (*Tax. Suppl.* under Panagaeini), *Coptocarpus* (*Tax. suppl.*, footnote under Oodini), and *Nototarus* (Part III, p. 185). These genera are all represented at low altitudes in tropical Australia (although the single individuals of *Craspedophorus* and *Coptocarpus* thus far found in New Guinea were in the mountains) and all are now wholly flightless in Australia as well as in New Guinea. They may have reached New Guinea without flying. However, their ancestors were probably winged not long ago and may have dispersed partly by flight.

[79] *Direction and ecology.* Direction of dispersal is correlated with ecology to only a limited extent. The principal ecologic groups of New Guinean Carabidae (mesophiles, hydrophiles, and arboreal forms) are all more Oriental than Australian in relationships and in probable origins. However, the mesophiles divide into two subgroups: those (more numerous) that live on the floor of rain forest are mainly Oriental; those (fewer) that live in open country including open eucalyptus woodland are mainly Australian. The latter, the mesophiles that live in relatively open, relatively dry areas in New Guinea, are apparently the only ecologic group of New Guinean Carabidae in which Australian relationships and probable origins do predominate. Because my ecologic division of the New Guinean fauna is rough at best, with many details in doubt, I see no point in attempting to find finer correlations between ecology and geographic origins.

[80] *Direction and altitude: mountain-hopping across the Malay Archipelago.* Direction of dispersal is not clearly correlated with altitude. Most Carabidae on the high mountains of New Guinea seem to have been derived from lowland forms on the island and not to have had independent geographic origins [90]. Of the few endemic high-mountain genera that do seem to have independent geographic relationships, *Analoma* and *Idiagonum* probably have Oriental and *Rhytiferonia* Australian ties, but their origins are far from clear. Less differentiated mountain-hopping carabids that have reached New Guinea are considered in more detail below. Doubtful cases which should be disposed of first include *Notagonum submetallicum* (see *Tax. suppl.*), a common, winged, southern Australian carabid which has been found at moderate altitudes both in tropical Queensland and in New Guinea; it may have begun to mountain-hop northward and westward, but if so, it has not gone far. *Craspedophorus, Physolaesthus,* and *Coptocarpus*, although thus far found only at middle altitudes in New Guinea, occur at low altitudes in tropical Australia and are probably not mountain-hoppers.

The three genera *Mecyclothorax* (Part I, pp. 498, 505; present part, *Tax. suppl.*), *Microferonia* (Part III, p. 18), and *Scopodes* (Part III, p. 197) have mutually similar distributions in the area under discussion. All these genera are now chiefly Australian, but all have also endemic species localized on mountains in New Guinea and in Java. (The distribution of *Mecyclothorax* is complicated by occurrence also on the Hawaiian Islands, etc., and of *Scopodes* by occurrence on New Guinea not only of one Australian-related species but of a second endemic stock which has radiated on the island, but these are added complications which do not affect the Australia-New Guinea-Java pattern.) The question is, have these genera mountain-hopped from Australia across New Guinea (and presumably Celebes) to Java, or are the isolated species on New Guinea and Java relicts left by

withdrawals (by partial extinctions) of the genera into Australia? I cannot answer this question, but at least in *Mecyclothorax* and *Scopodes* the New Guinean and Javan species seem fairly closely related to Australian species, and I think westward mountain-hopping is a possible explanation. All the pertinent New Guinean and Javan species of these genera are now flightless, but all three genera include winged species in Australia, and all may have dispersed by flight.

A reverse pattern of distribution is shown by *Sericoda* (present part, *Tax. suppl.*) and *Chydaeus* (Part III, p. 47), both of which are distributed as if they have mountain-hopped from Asia across the Malay Archipelago to New Guinea. In these cases direction of dispersal is clearer. An actual Oriental species of *Sericoda* reaches New Guinea and is still winged. And *Chydaeus* includes slightly differentiated species widely scattered on mountains on the Malay islands, some flightless, but others still retaining wings (for example, *C. bakeri* Andrewes on mountains in Luzon is still dimorphically winged).

The five cases of probable or possible mountain-hopping summarized in the two preceding paragraphs can be arranged according to apparent ages of dispersal, relative age being judged by state of wings and by amount of differentiation of the isolated species. *Sericoda,* with a winged species now extending from Asia to New Guinea, has presumably dispersed most recently. *Chydaeus,* with slightly differentiated species scattered from the Himalayas to the Philippines and New Guinea, and with wings still present in some insular forms, is presumably a little older. *Mecyclothorax* and *Scopodes*, each with well-differentiated, flightless species on Java and New Guinea, but with the Javan and New Guinean species apparently related to each other and related to specific Australian species, are presumably still older. And *Microferonia*, with Javan and New Guinean species also well defined and flightless, but perhaps less closely related to any particular Australian species (but the species of this genus need further study), may be oldest of all. This classification by age may be wrong in detail. However, it does seem probable that *Mecyclothorax, Scopodes,* and *Microferonia* dispersed in the Malay Archipelago before *Sericoda* and *Chydaeus* did, and it is at least possible that they represent stages in dispersal by a "sweepstakes" route across the mountains of the Archipelago from Asia to Australia. No single group of mountain-hopping Carabidae occurs along this whole route now. However, *Sericoda* and *Chydaeus* have covered most of the route (and an Asiatic stock of *Bembidion*, not related to the Australian *Bembidion*, has reached the mountains of Celebes—Darlington, 1959a), and *Mecyclothorax, Microferonia,* and *Scopodes* may have followed the whole route earlier, mountain-hopping from Asia to New Guinea and Australia, becoming extinct in Asia, and radiating in Australia especially south of the tropics. If so, the Javan and New Guinean species of these genera may be geographic relicts, and the special New Guinean group of *Scopodes* (Part III, p. 197, *Notes* under *Scopodes*) may represent a separate radiation of the ancestral stock which has paralleled the Australian radiation rather than being derived from it. This hypothetical history is diagrammed in Figure 14.

I do not know how these five genera really have dispersed. But I think the best way of attempting to decipher their histories is to put the cases together, see whether they fit a common pattern (as they seem to do), and see how that pattern compares with the distributions and apparent histories of other Asiatic-Australian Carabidae and of other animals and even of plants.

Among New Guinean Carabidae, *Demetrida* (Part III, pp. 140ff) *may* fit the pattern suggested for *Scopodes.* The ancestor

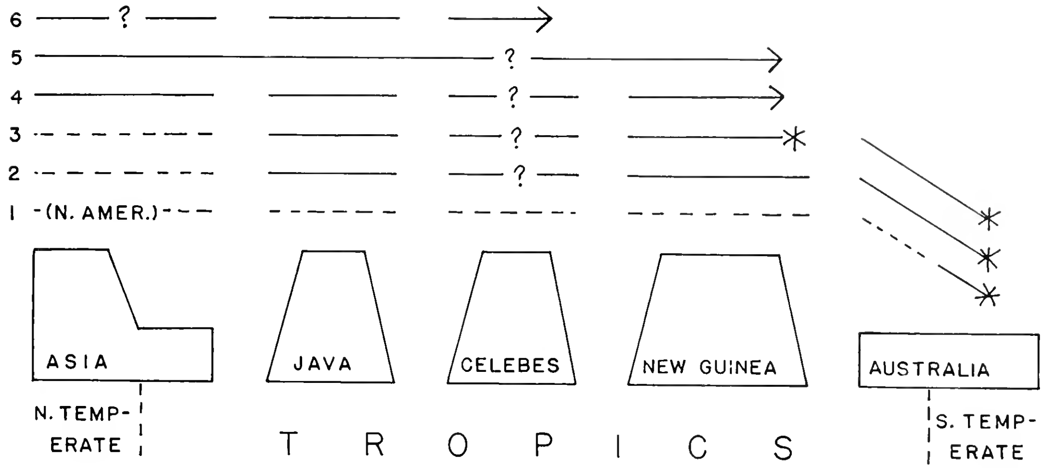

Figure 14. (Hypothetical) diagram of dispersal of successive mountain-hopping Carabidae from Asia to Australia. Broken lines indicate presumed past occurrences; solid lines, present occurrences. Case 1 represents Psydrini (included in Pterostichini in text) other than *Mecyclothorax*, now relict in North America and moderately diverse in Australia; 2, *Mecyclothorax*, now represented on mountains in Java and New Guinea and moderately diverse in south temperate Australia (and well represented in Hawaii, etc.); 3, *Scopodes*, now on mountains in Java and New Guinea with separate radiations in New Guinea and Australia; 4, *Chydaeus*, with slightly differentiated species on mountains from Asia to New Guinea but not Australia; 5, *Agonum* (*Sericoda*) *ceylanicum* (Motschulsky); 6, *Bembidion* of the *bryanti-pendelburyi* group (Darlington, 1959a), which has reached Java and Celebes but not New Guinea. See text for further details.

of *Demetrida* must have reached the Australian Region from some other part of the world, probably from Asia, since the genus does not have a subantarctic distribution. The New Guinean radiation of the genus (Part III, pp. 143–144), like that of *Scopodes*, may be a separate radiation of an original Asia-derived ancestor independent of the main Australian radiation. (However, I have scored *Demetrida* as probably having dispersed from Australia to New Guinea, see [74], Table 14.)

A pattern of distribution that seems basically similar is shown by the native murid rodents of the Australian Region, among some of which radiation has proceeded partly independently in New Guinea and in Australia. The subfamily Hydromyinae, for example, has diversified principally in New Guinea. In this case we know that the ancestral stock did come from Asia, and we can be reasonably sure that the ancestor of the New Guinean Hydromyinae was Asia-derived and did not come from Australia even by countermovement.

Another basically similar pattern is shown by a geographically notable genus of plants: trees of the genus *Nothofagus* (southern beeches) are well represented on the mountains of New Guinea as well as in south-temperate Australia, New Zealand, and South America. We know (from their pollen record) that the history of these trees in the southern hemisphere has been complex, but we can be reasonably sure that their ancestor came from the north. The numerous species on the mountains of New Guinea may therefore be products of radiation of an ancestor derived from Asia, not from Australia. (For further details and discussion see Darlington, 1965: 29–31 and other pages listed in index.)

In summary of Carabidae that seem to have mountain-hopped for considerable distances in the Malay Archipelago, *Sericoda* and *Chydaeus* (and *Bembidion*, to

Celebes) have clearly dispersed southeastward, from Asia, relatively recently; and *Mecyclothorax, Microferonia*, and *Scopodes* may have dispersed northwestward, from Australia, relatively long ago. However, all these genera may fit a common pattern of successive dispersals southeastward, from Asia toward Australia, with ancestral stocks later becoming extinct in Asia, and with separate evolutionary radiations sometimes (in *Scopodes*) occurring in New Guinea as well as in Australia. Some other Carabidae (notably *Demetrida*) may fit (a terminal stage of) this pattern. And some rodents (Hydromyinae) and some plants (notably *Nothofagus*) may have followed the same pattern of southeastward dispersal, extinction in Asia, and radiation in separate centers in New Guinea and Australia.

[81] *Direction and age*. Whether direction of dispersal is correlated with age (time of arrival) of different groups of Carabidae in New Guinea is an important question. It is conceivable that early arrivers might show different patterns of relationships and origins than later arrivers do, and the differences might indicate changes in the geographic or ecologic relations of New Guinea to the Orient and Australia. In the absence of a fossil record, age cannot be determined exactly, but it is at least a good working assumption that genera endemic to New Guinea (Table 13) are *relatively* old (but see [89]). Endemic genera of which the ancestors seem to have come from the Orient are *Perileptodes, Analoma, Lyter, Odontomasoreus, Tarsagonum, Idiagonum*, and *additional* chiefly mountain-living agonine genera, and those of which the ancestors seem to have come from Australia are *Rhytiferonia, Helluonidius* plus *Helluopapua* (one stock), and three endemic genera (perhaps only one stock) related to and perhaps derived from *Loxandrus*. (The relationships of *Tiferonia* and *Minuphloeus* are doubtful.) Among these presumably relatively older arrivers, therefore, Oriental stocks seem to be at least twice as numerous as Australian stocks, and the evidences of direction are clearer in the case of some of the Oriental stocks than of the Australian stocks, I think.

The carabid stocks that have radiated on New Guinea may also be *relatively* old. The radiation of agonines derived from *Notagonum*- and *Colpodes*-like ancestors is unique on the island. Their ancestors were Oriental. The uniqueness of this case lies not only in the amount of differentiation of species and genera at all altitudes (Part II) but also in the ecologic radiation (of mesophiles, hydrophiles, and even a few arboreal forms) that has occurred within the limits of New Guinea. A less striking radiation has occurred in the Pterostichini related to (derived from?) *Loxandrus*; this group is Australian in present relationships and may have been derived from Australia (but see [82]). The radiation of this group has apparently produced two or three endemic genera in New Guinea (*Haploferonia, Homalonesiota*, and *Nebrioferonia*, if the latter is recognizable) but few species, and its ecologic radiation has been relatively slight: its members are confined to low and middle (not high) altitudes, and the habitats occupied are only those associated with standing water (most *Loxandrus*), the banks of running water (*Nebrioferonia* and probably *Homalonesiota*), and the rain-forest floor (probably *Haploferonia* and *Loxandrus latus*).

The most striking multiplication of species on New Guinea has occurred in the genus *Demetrida*, which may be Australian in origin. Most members of this genus in New Guinea apparently live in the foliage of rain forest. Other species-radiations of Carabidae in rain-forest foliage have occurred in *Dolichoctis* of the *aculeata* and related groups, which may be derived from one Oriental ancestor, and in *Dicraspeda*, which is a mainly New Guinean genus (six rather diverse species on the island, all in lower-story rain-forest foliage) of unde-

termined ancestry. Among the Carabidae that live on tree trunks in rain forest, moderate species-radiations have occurred in *Catascopus* of the *wallacei* and perhaps other groups (Oriental in derivation) and in *Minuthodes*, which now occurs chiefly on New Guinea (nine species on the island) and of which the ancestor is undetermined but was probably Oriental rather than Australian. Other carabid stocks in which moderate radiations of species have occurred on New Guinea and of which the ancestors probably came from the Orient include several subgroups of *Tachys* (especially the *serra* group), some *Perigona, Trichotichnus,* and *Pogonoglossus*, all primarily ground-living mesophiles. And others of which the ancestors probably came from Australia include some *Clivina* (hydrophiles), *Agonochila* (arboreal), a special group of *Scopodes* (mesophiles, or on rotting logs), and *Helluonidius* (probably mesophiles). On the whole, the groups in which species-radiations have occurred on New Guinea probably include more Oriental derivatives than Australian derivatives, and the Oriental origins are clearer than the Australian ones, I think.

Facts and probabilities considered in the three preceding paragraphs suggest no obvious correlation between direction of dispersal and age of Carabidae on New Guinea. Some Carabidae have probably reached the island from Australia as well as from the Orient in both older and more recent times, but Oriental stocks have probably always been more numerous. This summary concerns only the direction of dispersal. Possible changes in rate of dispersal (numbers of stocks reaching New Guinea regardless of direction) from time to time are considered in [85].

[82] *Australian-American discontinuities.* A special pattern of distribution is exemplified by *Loxandrus* (Part I, pp. 498, 549–557), which occurs in two widely separated regions. The genus includes numerous species in Australia, four Australian-related species on New Guinea, and one slightly differentiated species on Celebes. This pattern suggests recent dispersal from Australia to New Guinea to Celebes. But *Loxandrus* is well represented also in the warmer parts of North, Central, and South America, and additional genera related to or derived from *Loxandrus* occur in the Americas as well as in Australia and New Guinea, but nowhere else in the world, as far as I know. The most likely explanation is that *Loxandrus* once occurred also in the Old-World tropics or at least in tropical Asia, that it reached Australia from Asia long ago, that it later became extinct in Asia, and that still later it made minor return movements from Australia to New Guinea to Celebes.

Most species of *Loxandrus* are hydrophiles; some of them are among the most aquatic of Carabidae, although some derived or related forms are more terrestrial. Another subaquatic genus of Carabidae, the oodine *Anatrichis* (Part III, p. 31), has a distribution that may correspond to that of an ancestral *Loxandrus*. *Anatrichis* occurs from southeastern Asia (including Japan, according to Uéno, personal communication) to Australia, and is widely distributed also in the warmer parts of the Americas. Both *Loxandrus* and *Anatrichis* are primarily tropical. They extend into moderate temperate areas but do not have the "subantarctic" distribution patterns of some other Carabidae that may have dispersed across Antarctica (for example, the Migadopini, Darlington, 1965: 35–37). The close relationship of the American and Australian *Loxandrus* has been established by modern methods of comparison (Moore, 1965), but *Anatrichis* needs study not only of species now assigned to the genus but of some other Australian species that may prove to be related (Darlington, Part III, p. 31, paragraph 3).

Two other, nonaquatic genera of Carabidae should be mentioned in this connection. The harpaline genus *Nemaglossa* or *Lecanomerus* (Darlington, Part III, p. 45) is supposed to occur in South America

and Australia, but the relationships of the South American and Australian forms need further study; whatever the earlier history of the group, the small species of *Lecanomerus* in New Guinea have presumably been derived from an Australian stock rather recently. And *Pseudaptinus* (*Thalpius*) occurs in the warmer parts of the Americas (numerous species) and in Australia (one species); this genus too needs study.

This pattern of Australian-American discontinuity occurs also in leptodactylid and hylid frogs, chelyid turtles, and especially marsupials. These animals do *not* have "subantarctic" distributions. All of them, like the Carabidae just discussed (*Loxandrus,* etc.), inhabit principally tropical and warm-temperate areas, and none of them occurs on New Zealand (except as recently introduced by man). The pattern may have been formed in somewhat different ways in different cases, but it is probably usually a relict pattern, the result of widespread extinctions in the main part of the world.

[83] *Summary of directions of dispersal.* New Guinean Carabidae have been found to include 173 Oriental and 120 Australian "geographic units" [58]. This finding (together with the fact that the carabid fauna of New Guinea seems to be mainly derivative, and not a source-fauna from which many groups have radiated geographically [70]) suggests that Carabidae have moved from the Orient to New Guinea more than from Australia to New Guinea. A comparison of the distributions of rapidly dispersing groups of Carabidae with those of more slowly dispersing groups [72] shows relatively strong Oriental relationships among the rapid dispersers, which again suggests movement mainly from the Orient toward Australia. Comparison of the distributions of Carabidae with those of mammals [73] suggests that many carabids have moved from the Orient to New Guinea and Australia while the terrestrial mammals were isolated in the Australian Region; a number of carabid species seem to have dispersed from Asia to Australia so recently that populations are not or not much differentiated on the two continents. Selected tribes, genera, and species of Carabidae that seem most clearly to show directions of movement [74, 75] include 89 groups that seem to have dispersed southeastward and only 39 groups that seem to have dispersed northwestward, and the disparity is greatest over the longest distance: 44 carabid stocks seem to have dispersed all the way from the Orient to some part of Australia, while only seven stocks seem to have dispersed from Australia to the Oriental area, and only one primarily Australian genus seems to have reached the mainland of Asia.

Before making a final summary, I want to re-emphasize the complexity of the situation, the difficulty of finding and assessing real evidence, and the tentative nature of the conclusions. Faunal movements are statistical, not co-ordinated one-way movements. They are the sums of very complex movements and countermovements of many families, tribes, genera, and species, which in turn are the sums of almost inconceivably complex movements of individuals. However, in spite of the difficulties and complexities, the evidences of net direction of movement of carabids in the Asiatic-Australian area are surprisingly good. The movements have been complex. Large numbers of Carabidae have apparently dispersed from Asia and the Oriental islands to New Guinea and Australia over a long period of time, while the numbers that have apparently dispersed from Australia to New Guinea and Asia are significantly smaller. Conclusions about direction are more or less tentative in single cases, but when all the cases are put together they form a pattern which (I think) is as a whole overwhelmingly probable: dispersal has been predominantly toward the southeast, from Asia toward Australia. At any one point along the route the preponderance of southeastern

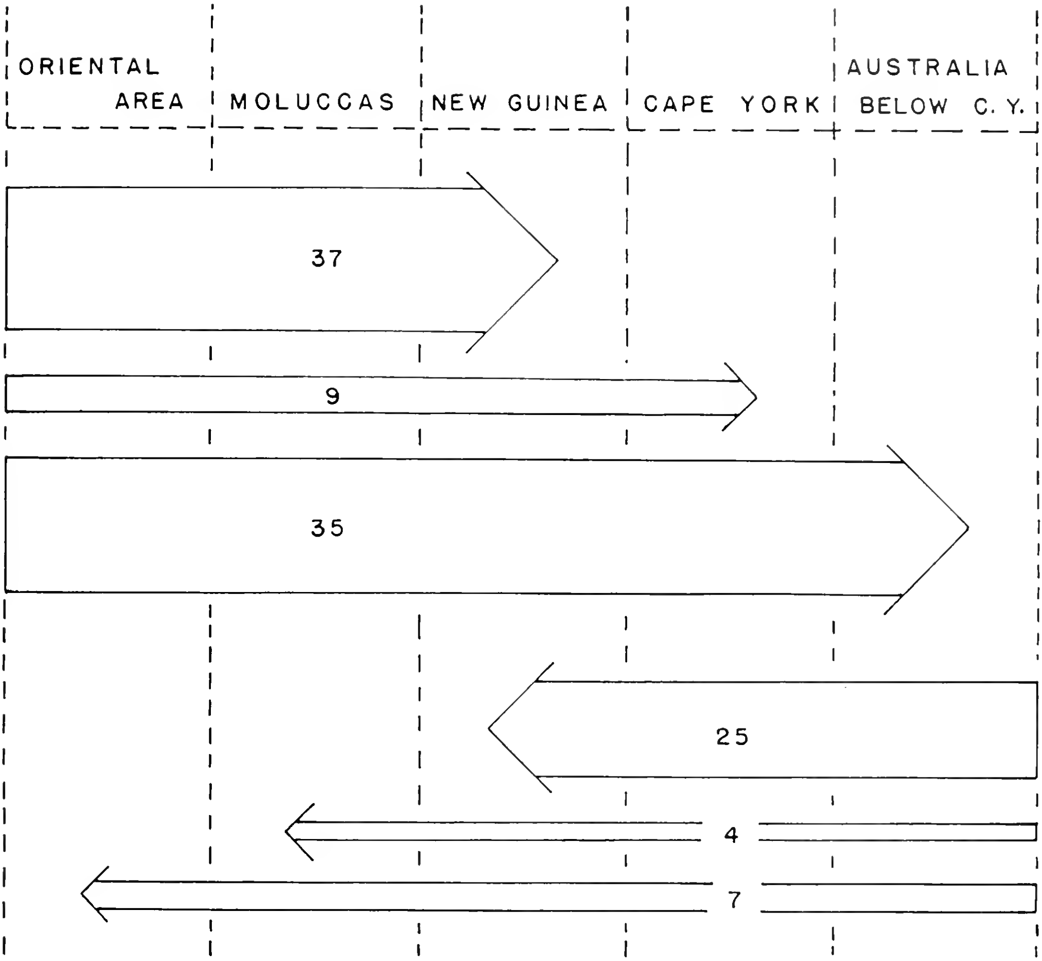

Figure 15. Diagram of apparent directional movements of Carabidae in the Oriental-Australian area. Lengths of arrows indicate distances moved; widths, numbers of stocks that seem to have made the movements; and numbers of stocks are given in figures on the arrows. See text for further details.

against northwestern movements may not have been very great, but over the route as a whole movements from Asia to New Guinea and Australia seem to have been several times more numerous than movements from Australia and New Guinea toward Asia. The resulting, complex but directional faunal movement is diagrammed in an oversimplified way in Figure 15.

My conclusion is that there has in fact been direction in the sum of movements of Carabidae in the Asiatic-Australian area: a continual flooding of Asiatic stocks into the Australian region, with much less movement of Australian stocks toward Asia, except for short distances. This process has probably been going on for a very long time, and is still going on. I think that it is only one feature—but a major one—of a complex pattern of directional movements which Carabidae are continually making over the world as a whole, but which (in the absence of a fossil record) are very difficult to demonstrate. The

apparent world-wide pattern of movements has been briefly described in [67].

One other deduction: if, as I suppose and as apparently must be the case if Carabidae are not to multiply without limit everywhere, additions to carabid faunas tend to be balanced by extinctions, then the movements toward Australia of many new Asiatic stocks must have been accompanied by withdrawals of many other Carabidae, the withdrawals tending to begin in Asia and to progress toward New Guinea and Australia. Some sort of balance between spreading of new groups and withdrawal of old ones would explain several characteristics of the New Guinean carabid fauna. It would explain, for example, the various cases in which New Guinean Carabidae seem to find their closest relatives in the Philippines; I have not stressed these cases, because most of the groups concerned are not well enough known taxonomically, but possible examples will be found under *Tachys exul* (Part I, *Notes* on p. 421), *Tiferonia* (Part I, *Notes* on p. 561), *Perigona erimae* (Part III, *Notes* on p. 12), and *Lebia papuella* (Part III, *Notes* on p. 88). The explanation, of course, is or may be that these groups once occurred on the Greater Sunda Islands or even on the continent of Asia, but have become extinct there as competing groups have moved from Asia into the archipelago. Another, more important characteristic of the New Guinean carabid fauna is that it seems to include few or no phylogenetic relicts [88, 89], and this may be not because New Guinea is a young island but because there has been a relatively rapid overturn of the fauna caused by the continual, massive influx of new stocks, chiefly from Asia, with extinction of older stocks. And some kind of balance between arrival of new stocks and progressive extinction of older ones may also explain the distribution of the "mountain-hoppers" [80], of which new stocks seem to be coming from the Asiatic end of the archipelago while older stocks may be "retreating" toward Australia (Fig. 14).

[84] *Barriers; filtering at Wallace's Line, Moluccas, and Cape York.* During dispersal across the Malay Archipelago, Carabidae seem to have encountered principal barriers at Wallace's Line, in the Moluccas, and between New Guinea and Cape York. These have probably been main filter points in the "sweepstakes route" (Simpson, 1940) which many Carabidae have followed, in one direction or the other, between Asia and Australia. These three barriers are of different sorts, and their filtering effects have probably been somewhat different.

At Wallace's Line, the barrier has been a gap of salt water—Makassar Strait—which has probably sometimes been narrower than now (perhaps only 25 miles wide in the Pleistocene) but which has separated Celebes from the continental shelf of Asia for a very long time. This is the first major barrier to eastward dispersal of Oriental stocks, and it is a relatively simple but effective barrier. Its effect on Carabidae has probably been primarily to block more sedentary forms while more vagile forms, especially small, winged, active ones, have often crossed it.

Among the Moluccas, too, water gaps have probably existed for a very long time. However, their filtering effect on dispersing Carabidae may have been less than the effect of Makassar Strait. The most sedentary, least vagile elements of the carabid faunas of both the Orient and Australia were probably filtered out by other barriers, so that the Carabidae that reached the Moluccas have been preselected for active dispersal. However, the Moluccas are relatively small islands. Their limitation of area has probably limited the numbers of species that could occur, and has probably given an extra advantage to dominant, successful stocks. The islands have therefore probably been a bottleneck through which only Carabidae with some degree of general dominance have been able to pass. (For further consideration of

the Carabidae of the Moluccas see [62]. And for discussion of dominance among Carabidae see [68].)

Finally, although New Guinea and Australia are separated by water now, they were broadly connected by land at times in the Pleistocene. Nevertheless only small fractions of the New Guinean and Australian carabid faunas crossed the land connection. The New Guinean rain-forest carabids that reached Cape York or farther into tropical Queensland were not very numerous and some of them are patchily distributed now (see [63] and Table 9). And the Australian open-country carabids that reached even southern New Guinea were not very numerous and were apparently severely filtered, for very few of the many flightless carabid stocks of Australia reached New Guinea. The barrier in this case seems to have been primarily ecologic, perhaps an alternation of areas of rain forest and open country like that which actually occurs on the Cape York Peninsula now, and which may have imposed (different) barriers to both rain-forest and open-country stocks, regardless of the direction of their dispersal.

That the three principal barriers to dispersal of Carabidae between Asia and Australia have probably acted in somewhat different ways is, I think, important. Together, however, they have had a common, net result: the accumulation on New Guinea of a carabid fauna composed almost entirely of small, winged, active carabids, many of them belonging to inherently successful, widely distributed, actively dispersing groups.

Among these actively dispersing groups, the hydrophiles are outstanding. Hydrophile Carabidae, that live beside water, are usually winged and do fly relatively often either to escape rising water or to maintain populations in shifting water-side habitats. Because they live in unstable, shifting habitats, they presumably have to maintain relatively large populations, and this may be an additional advantage to them in dispersal. Water-side habitats are to some extent independent of forest cover, so that Carabidae associated with them can disperse relatively easily across areas like present Cape York, where the forest cover is discontinuous. And presence of water probably gives some protection against extremes of climate, so that hydrophiles can cross climatic barriers relatively easily too. Hydrophile Carabidae do in fact seem to be exceptionally good dispersers. They have reached New Guinea in sufficient numbers not only to occupy their own habitats but also in several cases to invade the floor of rain forest, where they have apparently compensated for a deficiency of less vagile forms primarily adapted to the forest floor [97]. I have elsewhere (1959a; 1962a; 1965) suggested that not only the winged Australian *Bembidion* but also the now chiefly flightless and chiefly mesophile "*Trechus*" of south-temperate Australia have been derived from winged ancestors which crossed the tropics from Asia to Australia at low altitudes in water-side habitats.

[85] *Amount of dispersal, now and in the past.* Amount of dispersal—number of stocks dispersing between New Guinea and other areas regardless of direction—can be correlated with time, although the data are necessarily imprecise and the correlation is rather rough. The method is to count and compare the numbers of stocks of New Guinean Carabidae at three taxonomic levels: at the level of non-endemic species, which are shared with the Oriental area and/or Australia, and each of which has had its own separate dispersal; at the level of endemic species or groups of species not in endemic genera, counting only species or species groups that seems to have separate relationships outside New Guinea; and at the level of endemic genera or groups of genera, counting only those with separate relationships outside New Guinea. A general correlation of taxonomic level with time is assumed. That is, it is assumed that, in spite of

probable differences in rate of evolution of different stocks, nonendemic species have in general dispersed more recently than the ancestors of endemic species, which in turn have in general dispersed more recently than the ancestors of endemic genera.

The kind of unit to use for this purpose must be considered carefully. To count only stocks that show direction of dispersal [74, 75] would weight the results in favor of the more recent stocks, because clues that show direction are likely to be clearest in the stocks that have dispersed most recently. And the stocks to be counted now are not the same as my "geographic units" [31, 58]. The latter were designed to show existing relationships, and some wide-ranging stocks were therefore counted twice: *e. g.*, a New Guinean species that occurred also in both the Orient and Australia was counted as both one Or and one Au unit. Now, each stock will be counted only once. Also, in scoring "geographic units," I have counted only stocks with discernible geographic relationships, while now I shall count all stocks that seem independent within the New Guinean fauna, whether or not their geographic relationships are discernible. The resulting units might be called amount-of-dispersal units. They are designed simply to show the numbers of separate stocks that make up the existing New Guinean carabid fauna, correlated with taxonomic level and therefore presumably with age. Since the New Guinean carabid fauna is as a whole a relatively recent one [89], most amount-of-dispersal units probably represent movements into New Guinea, but this is not assumed in the calculation.

Table 16 summarizes the amount-of-dispersal units in the existing New Guinean carabid fauna. Before interpreting it, I should ask whether changes in my concepts of species and genera would significantly change the results—whether, if I "split" species and/or genera, the table would be significantly changed. I think the answer is that the counts would be changed, and that it might become necessary to tabulate units at additional taxonomic levels, including perhaps subgenera and natural groups of genera, but that if the classification were approximately phylogenetic, the table would still show many more dispersals at more recent than at the oldest level.

TABLE 16. SUMMARY OF AMOUNT-OF-DISPERSAL UNITS: NUMBERS OF SEPARATE STOCKS OF NEW GUINEAN CARABIDAE AT THREE TAXONOMIC LEVELS

	Nonendemic species	Endemic species and species groups in nonendemic genera	Endemic genera and groups of genera
Other than Agonini	128	±129	11
Agonini	9	±9	±5

Table 16 indicates that the existing New Guinean carabid fauna consists of many stocks that have not differentiated specifically, many that have become distinguishable species but not genera, but very few that have become distinct genera. This suggests that stocks that have dispersed more or less recently far outnumber those that dispersed longer ago. The difference in number of dispersals in proportion to time may have been greater than the figures show: the nonendemic species may have made their movements within a relatively short time; the endemic species may represent dispersals over a much longer time; and the endemic genera, a still longer one, so that the number of dispersals now represented in the New Guinean fauna by endemic genera may have been widely spaced over a very long period. This is diagrammed in Figure 16.

For this and other reasons actual amounts of dispersal cannot safely be calculated from Table 16. Nevertheless, the table does strongly suggest that one of two things has happened. *Either* amount of dispersal—number of groups moving into or out of New Guinea—has increased

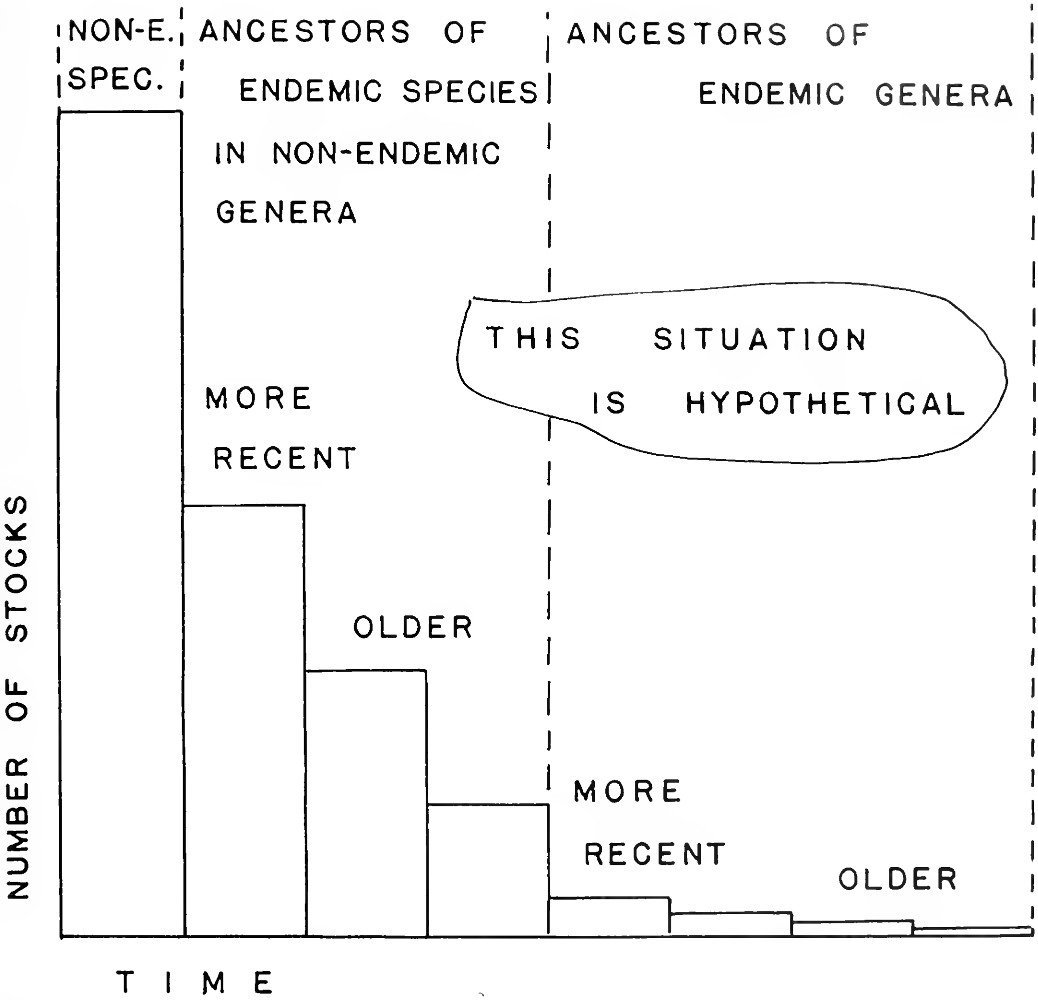

Figure 16. Histogram of numbers of stocks in relation to time in the existing New Guinea carabid fauna. Division of the ancestors of the endemic species and endemic genera into "more recent" and "older" categories is arbitrary. See text for further explanation.

enormously among Carabidae in relatively recent times. *Or* faunal overturn [68] has eliminated a large proportion of older stocks as new ones have come in. I prefer the latter explanation. It is consistent with the relatively recent nature of the New Guinean carabid fauna as a whole [89], and it is consistent also with my general hypothesis of dispersals and replacements of successive carabid groups over the world [67].

My conclusion is that, although the existing New Guinean carabid fauna is made up of many recently dispersed stocks and comparatively few old ones, this situation need not be the result of a recent increase in amount of dispersal. Carabidae may have been reaching New Guinea in numbers for a very long time, and the present fewness of old stocks may be due to extinction and replacement. I see no indication that New Guinean Carabidae form

two groups, one old and one relatively recent, separated by a time when few or none of the beetles reached the island. On the contrary, the concept of continual arrivals with continual overturns seems to me to fit the observed situation. There is therefore, as I shall say again [88], no initial starting point to be looked for in the accumulation of Carabidae on New Guinea.

Of course this simple conclusion about the dispersal history of New Guinean Carabidae covers an immense ignorance of details and also ignores many complicating factors and processes. For example, although I have noted that rates of evolution probably vary among different groups of Carabidae, I have not sufficiently emphasized how differences in rates of evolution may have affected some parts of the New Guinean carabid fauna. This is perhaps best shown by comparing the Agonini with the other carabids on the island. The Agonini are tabulated separately in Table 16. In general, the agonine figures conform to the table as a whole in that number of dispersals seems to have been greater among more recent than among older stocks, but in the case of the Agonini the correlation has been blurred by radiations on New Guinea, the radiations having proceeded to the point where the number of initial ancestors can no longer be determined with any accuracy. But I think the Agonini do fit the main pattern reasonably well, and that so far as they differ, the difference is due not to their being older on New Guinea but to their having evolved there either more rapidly or more diversely.

[86] *Summary of geographic origins of New Guinean Carabidae.* The history of Carabidae in the Asiatic-Australian segment of the world seems to have conformed in general (but of course not in detail) to the better documented history of vertebrates. The largest favorable area (the Old-World tropics, including tropical Asia) has apparently been the principal center of evolution and dispersal of dominant Asiatic-Australian Carabidae. The smaller and less favorable area of Australia has been a less important center. And the still smaller area of New Guinea has been least important in the evolution and dispersal of dominant carabid stocks.

Carabids have apparently been coming into New Guinea continually during a considerable period. There is no good evidence that arrivals were more numerous at some times than at others; arrivals have apparently been very numerous recently, but faunal overturns, with extinctions perhaps of many species, may have obscured the evidences of earlier arrival rates. Both Oriental and Australian stocks have probably reached New Guinea at all times. The incoming Oriental have probably always exceeded the incoming Australian stocks in number and importance, except that among terrestrial mesophiles living in relatively dry, relatively open country Australian arrivals have been more numerous at least recently. Otherwise, incoming Oriental stocks have probably been more numerous than Australian ones regardless of size of insects, regardless of wing-state (almost all were winged), in all main habitats, and at all altitudes, as well as at all times. There must also, I think, have been continual extinctions correlated with the arrivals, and if the arrivals have been more from the Orient than from Australia, extinctions ("withdrawals") also have probably tended to begin at the Oriental end of the area and proceed toward Australia. The result has probably been a gradual shift of major distribution patterns from Asia toward Australia, caused by the procession of both dispersals and extinctions in this direction. But the details of this pattern have been excessively complex and have been further complicated and partly obscured by local evolutions and radiations of some groups within New Guinea and elsewhere.

The broad movement of Carabidae from Asia toward Australia is, I think, part of

the world-wide pattern of evolution of successive dominant groups in the great, climatically favorable area of the Old-World tropics (Africa and tropical Asia) and of dispersal into smaller and/or climatically less favorable areas, with replacement of older by more recently dominant groups [67, 68]. And indications of extensive overturn in the New Guinean fauna itself [85] and evidences (not given here) that Carabidae have dispersed from New Guinea eastward to smaller islands, on which numbers of species of Carabidae are at least roughly proportional to area and isolation, are consistent with MacArthur and Wilson's (1967) theory of directional dispersal, faunal overturn, and faunal equilibrium on small islands. (In fact my diagram (Fig. 16) of the age structure of the New Guinean carabid fauna, although differently constructed, can be considered a model of faunal equilibrium comparable to the MacArthur-Wilson equilibrium model.) The New Guinean carabid fauna thus fits into and connects both the apparent worldwide pattern and the local insular pattern of evolution, dispersal, and faunal balance. I find this a very satisfying, unifying concept.

EVOLUTION

[87] *Evolutionary perspective.* For a thorough discussion of animal species and evolution, with the necessary background of modern biology and genetics, see Mayr, 1963. And for a careful statement of the apparent role of evolution in determining patterns of dispersal and resultant distribution patterns, see Darlington, 1965, Chapters 5 and 6. New Guinea can legitimately be treated as an evolutionary center of its own, but it should be remembered that it also has its place in worldwide evolution and dispersal patterns [67]. The patterns are apparently determined by the relative areas of different pieces of land, and by climate. The fact that New Guinea, although a very large island, is still much smaller than Asia or Australia has presumably limited its importance as a center of origin and dispersal of major groups [70], but has probably not limited either rate or diversity of evolution of species upon the island.

[88] *Evolution of New Guinean carabid fauna as a whole.* Geographic differentiation and overturn of Carabidae on New Guinea have been considered briefly in [85]. Now to be discussed in more detail are the evolution of the New Guinean carabid fauna as a whole, the differentiation and radiation of particular carabid stocks, and some general trends in the evolution of Carabidae on the island.

The starting point for discussion of the evolution of the New Guinean carabid fauna is the assemblage of ancestral stocks from which the fauna has evolved. These stocks were evidently pre-adapted in several ways. They were pre-adapted for dispersal across barriers, the pre-adaptations including usually possession of wings (the whole New Guinean carabid fauna is or may be derived from ancestors that were winged when they reached the island), small (or at least not very large) size, probably other characteristics of structure and behavior including the habit of flying actively, and often adaptation to water-side habitats. Some, but not all, of the initial stocks (especially some Agonini) had also characteristics—general adaptations [68]—that made for general dominance, *i.e.*, for success in a variety of situations.

The pre-adaptations that favor dispersal and the adaptations that favor continued existence in island habitats are partly different and opposed. For example, wings and flight pre-adapt a stock to dispersal, while existence in some habitats on some islands favors atrophy of wings. Or, for another example, small size favors dispersal, but continued existence on some islands may in some cases (perhaps on Madagascar [20] but apparently not on New Guinea) favor increase of size. There may therefore

be a reversal of direction of selection and adaptive evolution after carabids reach an island, and this in part explains the extraordinary distinctness of many insular carabid faunas, including that of New Guinea especially at higher altitudes. To restate this important generalization in different words: dispersal from a source fauna to an island selects as ancestors of the island fauna fractions of the source fauna that happen to be pre-adapted for dispersal; but when these fractions evolve and radiate to form a whole fauna on the island, direction of selection is partly reversed, and the new fauna that evolves is likely to be very different from the source fauna in gross taxonomic composition as well as in many details.

Most of the ancestral stocks from which the New Guinean carabid fauna has evolved apparently reached the island at low altitudes and were adapted to lowland tropical habitats. Carabidae in such habitats, including tropical rain forest, often do seem to be small and winged [21]. This may be partly because carabid populations in these places tend to have "patchy" distributions [22] maintained by continual redispersals, so that the characteristics that pre-adapt for dispersal to an island also pre-adapt Carabidae to survive in lowland tropical habitats on the island. However, dispersal across a tropical archipelago not only strongly selects small, winged, lowland Carabidae but also probably has other filtering effects. Carabidae tend to be more active and more liable to dispersal in some habitats than in others, so that some ecologic groups disperse more readily and reach islands more often than the others do. Dispersal may be more rapid in relatively open country than in heavy forest. And carabids that are associated with water apparently disperse more readily than those that are not. The multiplication of species in some groups (*e. g., Demetrida,* see Part III, p. 140) in foliage and on tree trunks in rain forest in New Guinea suggests an initial deficiency of carabid stocks in these habitats, the deficiency being compensated for in part by multiplication of the comparatively few rain-forest stocks that have reached the island and in part by ecologic shifts of hydrophiles onto the rain-forest floor. This is consistent with the general rule stated by Wilson (1961) for the ants of New Guinea and other islands: that dispersals tend to occur in marginal habitats, and that after dispersal some stocks penetrate the rain forest and evolve and diversify there. Water-side habitats apparently are marginal so far as the rain forest is concerned. They are certainly less stable and also more widely distributed than habitats on the ground in rain forest. Carabidae that live beside water do seem to disperse relatively easily and do apparently undergo ecologic shifts onto the rain-forest floor [84, 97].

So, I take as the starting point of evolution of the New Guinean carabid fauna an initial assemblage of immigrants: small, winged, dispersible forms concentrated at low altitudes and adapted to existence in the lowland tropics, but "disharmonic" taxonomically, with a surplus of Agonini, and disharmonic also ecologically, with a surplus of hydrophiles but a moderate shortage of stocks living in rain forest and an extreme shortage of stocks adapted to mountain habitats. I call this an initial assemblage, but I do not think of it as having a single starting point. It was, rather, a changing or evolving continuum, a sort of faunal germ plasm, of relatively unspecialized forms. We do not know when it began. We do know or at least suppose that it has been continually changing by "faunal overturn," by arrival of a succession of new stocks and extinction of old ones, although some of the older stocks have been evolving and radiating even while new ones have been continuing to arrive. I think that overturn has probably been so extensive as to destroy most or all of the earlier stages of accumulation of Carabidae on New Guinea. There are two reasons for thinking that overturn has been extensive

First, many species of Carabidae have reached New Guinea so recently that they are not yet differentiated there, and if one accepts the idea of faunal balance as applying to all faunas everywhere (except extremely young or very isolated ones), New Guinea must have lost many older stocks to compensate for the arrival of new ones. And second, the New Guinean carabid fauna seems to possess no striking evolutionary or geographic relicts, nothing that seems very old, or taxonomically isolated, or geographically very distant from its relatives, as if all really old members of the changing and evolving fauna have been eliminated. New Guinea possesses no endemic tribes; endemic genera are few; and all of them have or may have relationships with other Carabidae still existing in the Oriental or Australian Regions. If such genera as *Mecyclothorax* and *Loxandrus* are geographic relicts, they have survived primarily in Australia rather than in New Guinea. Australia and New Zealand possess a number of geographically isolated carabid stocks (*e. g.*, the "carenums" [35] and various Pterostichini [39] in Australia, and certain stocks with apparent northern relationships on New Zealand [89]) which may have come long ago via New Guinea but are not represented there now, and this is at least consistent with disappearance of older stocks on New Guinea. I shall note again this point—the apparent absence of relicts among New Guinean Carabidae—in considering the relative age of the fauna [89]. The actual rate of overturn (arrivals/extinctions) can perhaps be calculated eventually by formulae something like those devised by MacArthur and Wilson (1967). But neither existing data nor my mathematics are adequate now.

To summarize: the "initial assemblage" from which the New Guinean carabid fauna has evolved should be thought of as a changing continuum of which we cannot see the beginning but only a relatively recent segment.

From this changing continuum different carabid stocks on New Guinea have evolved to different extents and in different ways. The most striking processes have been multiplications of species and ecologic radiations. These processes are further discussed below [91, 92]. As far as the fauna as a whole is concerned, the principal results of the multiplications and radiations have been greatly to increase the number and diversity of both ground-living and arboreal Carabidae in rain-forest habitats, and especially to form on the higher mountains of New Guinea a complex alticoline fauna which is ecologically like the carabid faunas of mountains elsewhere (Darlington, 1943) but which consists largely of genera and species which have apparently evolved on and are confined to the island. Most of this alticoline fauna seems to have been derived primarily from the surrounding lowlands of New Guinea, by differentiations of alticoline stocks from lowland ancestors and by ecologic radiations especially of Agonini at high altitudes. The "mountain hoppers" [80] that have reached New Guinea make up a comparatively small part of the mountain carabid fauna [90].

So, the New Guinean carabid fauna can be thought of as derived from a changing continuum of relatively unspecialized, small, winged, lowland ancestors, including many hydrophiles and some relatively unspecialized Agonini, which have been coming in over a long period of time, and from which have evolved on New Guinea a great, partly endemic rain-forest fauna and a diverse, unique mountain fauna. The complexity of this process and of the whole carabid fauna it has produced is, of course, far beyond what I can describe or even satisfactorily indicate.

[89] *Relative age of the New Guinean fauna.* If the New Guinean carabid fauna has evolved not from an initial set of ancestors beginning at one point of time but from a constantly changing accumulation of ancestors, including relatively general-

ized Agonini, to which additional incoming stocks have continually been added while other stocks have continually been eliminated, an exact determination of the age of the fauna may be impossible even in theory, and absence of a fossil record makes dating it in terms of geologic time impossible in practice in any case. We do not know the geologic age of New Guinea; we do know that some of the mountain ranges are geologically recent, but we do not know how long a significant piece of land has existed where New Guinea now is; we do not know when Carabidae were first able to reach and exist on proto-New Guinea, if there was one; and we do not know whether the ancestors of the existing fauna were the first carabids on the island or whether they were preceded by others that have disappeared during faunal overturns. However, although we cannot determine absolute age, we can say something about the relative age of the New Guinean carabid fauna, its age in relation to the faunas of other land areas.

Both tropical Asia and Australia have carabid faunas that include noteworthy evolutionary and geographic relicts. Tropical Asia, for example, has an endemic tribe (Idiomorphini), as well as at least a few genera which are isolated taxonomically and/or widely separated geographically from their closest relatives (for example, *Mouhotia*, a genus of enormous, flightless scaritines confined to the Indo-Chinese Peninsula), and Australia has two endemic tribes (Agonicini in the southeast and Cuneipectini in the west), as well as *Pamborus*, a striking endemic assemblage of large scaritines [35], diverse and isolated pterostichines (and psydrines) [39], and others. New Guinea has no comparable relict or isolated Carabidae. But perhaps no island, not even a large one, should be compared with continents.

A more significant comparison can be made with the carabid faunas of New Caledonia and New Zealand. New Caledonia has several genera of Carabidae so distinct that their relationships are doubtful, or so isolated geographically that their dispersal routes are lost. For example, the New Caledonian genus *Cyphocoleus* (eight species) is so distinct that it is not clear whether it belongs in the Agonini or in the Lebiini, and the New Caledonian scaritine genus *Anomophaenus* (eight species) is not related to anything now existing in Australia or New Guinea, its nearest relatives being (perhaps) in tropical Asia. And New Zealand has an endemic tribe (Zolini), an extraordinary relict genus (*Maoripamborus*, related to the Australian *Pamborus*), and endemic groups of Trechini, Agonini (Sphodrini), and perhaps *Bembidion* of which the closest existing relatives seem to be in *north*-temperate areas (for discussion of these cases see Darlington, 1965: 64). In contrast, New Guinea, although it has a much larger carabid fauna than either of the other islands, has no endemic tribe of Carabidae and relatively few (few in proportion to the size of the fauna) endemic genera, and all of the latter have or may have relatives in adjacent areas, in either the Oriental Region or Australia. I conclude that the carabid fauna of New Guinea is more recent in its origins than the faunas of tropical Asia or of Australia or of New Caledonia or New Zealand.

It should be re-emphasized that the relative ages of the faunas do not necessarily indicate the relative ages of the islands. What the relatively recent age of the New Guinean carabid fauna probably does indicate, I think, is that, because of the greater accessibility of the island Carabidae have flooded into New Guinea in much greater numbers than into New Caledonia or New Zealand, and that faunal overturns have therefore been more rapid and more thorough in New Guinea.

[90] *Evolution of the mountain fauna*. The general characteristics of the mountain carabid fauna of New Guinea are the same as those of mountain faunas elsewhere (Darlington, 1943). The mountain

species are indicated on my data sheets [16]. Species are relatively few in any single mountain faunule, but geographic replacements are frequent, and the total number of species on all the mountains of New Guinea is very great [19]. The size range of the mountain species is within the range of the lowland species but with a single mode at 9–9.5 mm, which is larger than the larger of the two lowland modes; but this is apparently due not to increase of size of Carabidae on the mountains but to failure of many small forms to reach high altitudes [20]. Incidence of species with atrophied wings increases with altitude, reaching about 95 per cent on the highest mountains; this is a result of atrophy of wings (and multiplication of species following wing atrophy) in New Guinea, not of accumulation of wing-atrophied stocks from outside the island [21–23]. Ecologically, most of the mountain species are mesophiles, of which the majority live in wet montane forest, fewer in grassland above the forest zone; a few are hydrophiles living on the banks of mountain streams; and a few are arboreal [24, 25]. The effects of altitude on Carabidae [26] may be partly direct, but indirect effects seem more important and probably include climatic control of vegetation, limitation of areas, reduction of competition with ants, and presumably other factors.

The mountain carabid fauna of New Guinea, of which some characteristics are reviewed above, is composed of very many separate stocks, derived mostly from the surrounding lowlands, over a considerable period of time as indicated by their different degrees of differentiation. The most recent movements, probably still going on, may be of lowland species into mid-altitude grass areas deforested by man [26]. Many other of the 161 species of Carabidae known to occur both below 500 and above 1000 m [19] may also have moved (spread) from the lowlands to mid-altitudes recently. In a few cases altitudinal differentiation has apparently just begun, for example, in *Brachidius crassicornis* (Part I, p. 508; *Tax. suppl.*), in which mountain individuals are relatively large; in *Prosopogmus garivagliae* (Part I, p. 537), in which lowland and mountain individuals differ slightly in elytral striation and width of intervals; and in *Trichotichnus nigricans* (Part III, p. 52), which is fully winged at low altitudes but dimorphically winged on the Bismarck Range. In many other cases differentiation has proceeded to the point where mountain-living (usually mid-altitude) species now exist in genera which are well represented also in the lowland fauna. Such genera in which the mountain-living species are still winged include (this is far from a full list) *Tachys, Notagonum* (see also below), *Colpodes, Iridagonum, Trichotichnus, Harpaloxenus, Hyphaereon, Catascopus, Agonochila,* and especially *Demetrida.* A few primarily winged lowland genera include mountain species in which the wings have atrophied; for examples see *Clivina kubor* (*Tax. suppl.*), *Lesticus* (Part I, p. 521), and *Notagonum ambulator* (*Tax. suppl.*). And differentiation has gone still further in some other genera (chiefly of Agonini, Part II) which are now confined to the mountains of New Guinea and of which all species now have atrophied wings, although they are probably descended from winged lowland ancestors.

These (incomplete) details are, I hope, enough to give some idea of how the mountain carabid fauna of New Guinea has evolved, primarily by accumulation of many stocks derived from the surrounding lowlands, and by their differentiation at and adaptation to high-altitude habitats and in some cases their further geographic differentiation and ecologic radiation on different mountain ranges.

The additional Carabidae that seem to have reached the mountains of New Guinea from outside the island, by "mountain-hopping" [80], have apparently done so at different levels. *Agonum* (*Sericoda*)

ceylanicum (*Tax. suppl.*) and *Notagonum submetallicum* (*Tax. suppl.*) occur at mid-altitudes; *Microferonia* (Part III, p. 18), in the highest montane forest; and *Mecyclothorax* (Part I, pp. 498, 505; present part, *Tax. suppl.*), *Chydaeus* (Part III, p. 47), and *Scopodes altus* (Part III, p. 198), above the forest zone. The mountain-hoppers thus make up an insignificant fraction of the carabid fauna at intermediate altitudes but a relatively larger fraction of the small faunules on the exposed summits of the highest mountains (see [19] and Table 2). Perhaps climatic barriers keep most lowland tropical groups of Carabidae from populating these summits, and perhaps "mountain-hopping" occurs most often at this altitude, where carabids adapted to temperate climates are exposed to wind.

I am not sure that I have sufficiently stressed the *isolation* of the mountains of New Guinea from the rest of the world so far as Carabidae are concerned. It is emphasized by the fact that no *Bembidion* [36] and no *Trechus* [37] have reached these mountains, although these genera (in a broad sense) are dominant on mountains in the northern hemisphere and have invaded or are invading mountains in southern Australia and Tasmania. It is of course the isolation of the mountains, the difficulty which Carabidae adapted to montane habitats in other parts of the world have had in reaching them, that has allowed an independent mountain fauna derived mainly from the surrounding lowlands to accumulate and evolve, with only minor additions received directly from outside the island (preceding paragraph).

As to age, the mountain carabid fauna of New Guinea is not necessarily very old. The mountains themselves are apparently geologically young [17], and the distribution of Carabidae on them is essentially orderly, as if the insects have evolved (as mountain-living forms) on the mountains that now exist. If the beetles had evolved on older mountains and occupied the present ones later, I would expect patterns of distribution to be much less orderly. A few endemic, mountain-living genera such as *Rhytiferonia* (Part I, p. 533), *Analoma* (=*Paraloma*, Part I, p. 538), and *Idiagonum* (Part II, p. 229) are relicts of a sort, since they do not seem to have ancestral stocks still existing in New Guinea, but they are not very isolated taxonomically, and I think they are likely to have been derived from lowland New Guinean ancestors that have disappeared during overturns of the lowland fauna [89]. Some overturn may have occurred on the mountains too, but the orderliness of distribution patterns suggests that replacements have not been extensive.

The enormous ecologic shift that Carabidae (and other insects) make in moving from the tropical lowlands to higher altitudes in New Guinea should be re-emphasized. It involves formidable changes of climate, of vegetation, and probably of micro-habitats, and often great reduction of the areas inhabited by populations. Limitation of area may be the most important of these factors [22]. It presumably affects the structure of populations, which in turn affects number of species, state of wings, and so forth. The mountain Carabidae of New Guinea show other diverse specializations. The body form is often strikingly modified (see figures on pages 263, 295, 312). Loss of setae is common [95]. The eyes are often reduced, becoming either small and flat or small and abruptly prominent (see Part II, pp. 95–96, and [98]). The mandibles are sometimes modified, becoming either long and curved or exceptionally slender and almost straight, presumably in adaptation to special foods. In a few cases, for example *Brachidius crassicornis* (Part I, p. 508) and *Notagonum dentellum* with subspecies *chimbu* (Part II, p. 149), an increase of size of mountain as compared with lowland individuals has been noted, but in *Lesticus* (Part I, p. 521) the mountain species are

TABLE 17. NOTABLE SPECIES-RADIATIONS AMONG NEW GUINEAN CARABIDAE, EXCLUDING AGONINI (FOR WHICH SEE [92])

Demetrida: 59 known species on New Guinea from 1 or few ancestors; at low and moderate altitudes, chiefly in foliage in rain forest; this case put first and separated for emphasis

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Clivina: probably minor radiation of *australasiae* and some other groups; chiefly at low altitudes; fossorial, mostly in wet places

Tachys: minor multiplications of species; chiefly at low altitudes; chiefly on the ground in rain forest (*serra* group) and beside running water (*politus* group, in part)

Perigona: probably minor radiation of species in subgenus *Trechicus*; at low altitudes; in leaf litter in rain forest

Trichotichnus: moderate species radiations; at low and middle altitudes; especially on the ground in rain forest

Minuthodes: primarily New Guinean genus (9 species on the island); chiefly at low altitudes; on tree trunks etc., in rain forest

Catascopus: moderate radiation in *wallacei* group (a primarily New Guinean group of 5 species) and perhaps some other groups; at low and middle altitudes; on tree trunks in rain forest

Dolichoctis: moderate radiation especially in *aculeata* + *polita* groups (about 10 interrelated species on New Guinea); chiefly at low altitudes; in lower-story foliage in rain forest

Agonochila: 7 apparently interrelated, small species on New Guinea; chiefly at mid-altitudes; habitat unreported but probably arboreal

Scopodes: moderate species-radiation (7 interrelated species in special New Guinean group); at mid-altitudes; probably on logs etc., in montane forest

Dicraspeda: genus primarily New Guinean (6 rather diverse species on the island); chiefly at low altitudes (1 at mid-altitudes); all probably in under-story foliage of rain forest

Pogonoglossus: 9 species on New Guinea, interrelationships not determined but probably in part product of local radiation; at low and middle altitudes; in leaf litter etc., in rain forest

Helluonidius-Helluopapua: probably related genera with together 6 species probably product of radiation on New Guinea; at low and middle altitudes; habitat not reported but probably on the ground or possibly on tree trunks

smaller than the lowland ones, and in most cases I find no general increase in size in comparing the same or related species at different altitudes (see first paragraph of present section, and [20]).

The mountains of New Guinea are, I think, a magnificent natural laboratory for the study of evolution. Selective forces are probably intense there; the adaptive changes that occur are profound; and populations are probably often confined to limited areas within which they can be measured and perhaps even manipulated. As a taxonomist doing second-stage faunal work (Part I, pp. 328–330), I can emphasize this situation, but I cannot go further in investigation of it.

[91] *Evolution and adaptation of separate carabid stocks.* Within the main process of continual accumulation, survival, evolution, extinction, and overturn of the fauna as a whole, some particular carabid stocks have had notable evolutionary histories on New Guinea. In some cases the histories have involved mainly multiplications of species, in others more or less extensive adaptive radiations into new habitats.

Speciation with relatively little adaptive radiation seems to have occurred in *Demetrida* (Part III, p. 140), in which 59 known species have evolved on New Guinea from one or a very few ancestors. Some species of this genus have differentiated at different altitudes and probably in slightly different niches, but the ecologic range of the genus as a whole is (in New Guinea) probably confined to foliage chiefly in rain forest, with perhaps a minor invasion of grass at high altitudes. Less extensive but still notable species-radiations that have occurred partly or wholly within the limits of New Guinea are listed in Table 17. Most of them have occurred in rain forest. Note that Agonini are not included in this table; their radiations will be considered separately [92].

Adaptive radiations into new habitats are (except in the Agonini) fewer and less easy to demonstrate than multiplications of species. The extent of adaptive radiation among New Guinean *Demetrida*, for example, although probably not great, is in fact unknown, because the actual habitats of many of the species are unknown. In two other groups limited adaptive radiation is suggested but not yet actually known. In one of them, *Dicraspeda* (Part III, p. 210), the six species all occur in understory foliage of rain forest, but striking differences in size, color, and tarsal structure suggest that different species occupy different niches within the rain-forest-foliage habitat. And in *Helluonidius/Helluopapua* the six known species exhibit such striking differences in tarsal and antennal structure as to suggest ecologic differentiation, although the habitats of the species are unknown.

A limited but noteworthy ecologic shift from water-side habitats to the floor of rain forest seems to have occurred in several stocks of New Guinean Carabidae (cf. [84]). In *Platycoelus*, for example (Part I, pp. 541ff), most species are found in wet places, but *P. depressus* apparently lives in leaf litter on the ground in rain forest, and it is the only member of the genus in which the wings have begun to atrophy (the species is now ±winged), loss of wings probably being correlated with shift from a less to a more stable habitat. In *Loxandrus* (Part III, pp. 549ff), most species are closely associated with water, but *L. latus* probably occurs in rain-forest leaf litter; this species too is ±winged, apparently becoming flightless in the more stable habitat. In *Notagonum*, most species are found in wet places (or in montane habitats), but *N. spinulum* (Part II, p. 157) lives in rain-forest leaf litter; it is still fully winged. And in the mainly subaquatic genus *Oodes*, *O. terrestris* (see *Tax. suppl.*; = *laevissimus* of Part I, p. 34) has left the water and now occurs commonly and (in my experience) exclusively in rain-forest leaf litter. Wing reduction may have begun in this species (the wings are slightly reduced in some individuals), and two related species localized in different places in New Guinea are –winged, suggesting that geographic differentiation of the flightless *terrestris* stock has begun.

In two other cases species of Carabidae belonging to primarily hydrophile groups have become adapted to drier habitats in opener places rather than in rain forest. They are *Tachys aeneus* (Part I, p. 463) and *Egadroma robusta* (Part III, p. 71). However, their ecologic shifts may not have occurred in New Guinea, for the species concerned have extensive ranges outside as well as inside the island.

[92] *Agonine radiation on New Guinea.* The radiation of Agonini on New Guinea (Part II; present part, *Tax. suppl.*) goes far beyond that of any other group of Carabidae. Although a number of agonines have probably reached the island independently from time to time (a few species of *Arhytinus*, *Euplenes*, *Dicranoncus*, *Lorostemma*, *Agonum*, *Notagonum*, and *Colpodes* are not or not much differentiated and have probably come in recently), the great majority of the 160 species of the

tribe known on New Guinea have apparently evolved from very few ancestors. The principal ancestors were generalized, tropical, lowland agonines of moderate size, fully winged, and with full complements of standard setae. (In fact it is still true that *all* Agonini that occur at low altitudes on New Guinea are winged, and almost all the lowland species still have full counts of setae.) Such agonines, placed in the "genus of convenience" *Notagonum*, are still numerous especially at low altitudes in New Guinea. They are presumably derived from Oriental stocks, but the details of their relationships have not yet been worked out. Such relatively unspecialized stocks of agonines have entered every ordinary New Guinean habitat, and have evolved in many directions. At low altitudes, different hydrophiles have become adapted to deep swamps, to the banks of rapidly flowing streams, and to various more-ordinary water-side situations, and some (*Iridagonum* as well as *Notagonum spinulum*) have invaded leaf litter on the floor of rain forests. (Some are arboreal, but most arboreal agonines at low altitudes in New Guinea, including several *Colpodes*, have probably reached the island independently and are not derived from *Notagonum*-like ancestors.) From the lowlands, different Agonini have evidently invaded the mountains at different times. Some mountain-living forms are still only subspecifically differentiated from their lowland relatives (*e. g., Notagonum dentellum chimbu*, Part II, p. 149); others are distinct species of primarily lowland genera (*e. g., Notagonum altum*, Part II, p. 144); others have differentiated generically, often changing their form and often losing their wings and some of their standard setae. Some of the alticoline genera have speciated or even radiated ecologically in small areas at high altitudes. The best known example is *Nebriagonum* (Part II, p. 235), of which six species now occur on the Bismarck Range, some of them being mesophiles, some hydrophiles, and one subarboreal; this ecologic radiation has apparently occurred within the limits of the Bismarck Range. Of other mountain-living genera that may have been derived from *Notagonum*-like ancestors, *Gastragonum* apparently includes mesophiles living in relatively open places; *Altagonum, Montagonum, Laevagonum*, and *Fortagonum*, mesophiles living mostly in montane rain forest; *Potamagonum*, hydrophiles living beside turbulent mountain brooks; and *Maculagonum*, perhaps subarboreal species living at least partly in grass. This is a very inadequate description of the extent and diversity of radiations of Agonini in New Guinea. In fact, the habitats and habits of most of the mountain species are unknown (but can often be deduced from the insects' structure or from what is known of the localities where they occur), and very many—perhaps hundreds—of high-mountain species probably still remain to be discovered.

Although the Agonini have diversified so much more than other Carabidae on New Guinea, I do not think they need be older than the others. Their present patterns of complex and often close interrelationships suggest an explosively radiating group rather than an old one. And their patterns of distribution on the mountains of New Guinea suggest rapid evolution *in situ*, with clusters of distinct but related species and even small genera often confined to single supposedly geologically recent ranges. I therefore think that the extraordinary radiation of Agonini on New Guinea indicates not age but inherent dominance derived from characteristics—general adaptations [68]—which pre-adapt the insects for success in diverse situations. What these general characteristics of Agonini are, whether structures or physiological processes or behavior patterns, I cannot even guess. Study of the living insects both in their habitats and in the laboratory may suggest them.

[93] *Evolutionary trends: not toward increase of size*. Several different, presum-

ably adaptive evolutionary trends shared by several or many different carabid stocks on New Guinea can be detected, and one trend that has *not* occurred is noteworthy too.

A trend toward increase of size has *not* occurred in evolution of Carabidae on New Guinea. I base this statement on comparisons (made during the course of my taxonomic work) of many New Guinean Carabidae with closely related forms in southern Asia and in Australia. The average size of mountain-living Carabidae on New Guinea is greater than the average size of lowland forms, but this is apparently a result of a deficiency of small species at high altitudes, not a result of increase in size during evolution of mountain-living stocks [90]. Certainly no trend toward gigantism has occurred among Carabidae at any altitude on New Guinea. There is no indication here of evolution toward the situation on Madagascar, where very large carabids dominate the fauna.

[94] *Atrophy of wings and associated trends.* A trend toward atrophy of wings is conspicuous among New Guinean Carabidae, but only on the mountains. Wing atrophy is insignificant among the lowland forms, but increases with increasing altitude until something like 95 per cent of the carabids on the highest mountain-tops have atrophied wings. The state of wings, the incidence of wing atrophy, and the process of atrophy have already been sufficiently discussed [21–23]. Now, I want merely to re-emphasize two points. The first is that the atrophy process is apparently inhibited in most cases at low altitudes on New Guinea, so that the lowland carabid fauna continues to consist almost entirely of small, winged species. Such species are pre-adapted to dispersal [88]. Their predominance at low altitudes in New Guinea might mean that small, winged carabid stocks come in in such numbers, and that the lowland fauna is overturned so rapidly, that species do not have time to evolve either large size or flightlessness at low altitudes on the island. However, I think it is more likely that small, winged Carabidae dominate the lowland fauna in New Guinea simply because they are well adapted to conditions there, as they are to conditions at low altitudes in the tropics on continents [21].

The second point is that the very strong trend toward atrophy of wings at high altitudes has been accompanied or followed by secondary trends. Some are direct results of wing atrophy, which directly causes or favors shortening of the metathorax and co-aptive shortening of the elytra and (sometimes) narrowing of the elytral humeri. The elytra also tend to become locked together along the suture. Less direct effects of wing atrophy include, often but not always, a reduction in size of eyes. The changes of form and reduction of eyes together tend to produce a more compact, less active carabid which often can be recognized at a glance as flightless.

[95] *Loss of setae.* A strong trend toward loss of certain setae (specified below) parallels atrophy of wings. Loss of setae, like loss of wings, is correlated with altitude, and in fact the two processes are to some extent correlated with each other. Setae are not often lost by active, winged Carabidae even at considerable altitudes; no loss of setae has occurred among the (winged) alticoline species of *Notagonum*, and most of the numerous (winged) alticoline species of *Altagonum* have lost only one pair of pronotal and sometimes one pair of elytral setae (although additional setae have disappeared in a few species of this genus). But in alticoline stocks that have lost their wings and have been otherwise modified [94], setae have disappeared more often and in a variety of patterns.

The setae concerned are the two pairs of supraoculars, the two pairs of lateral pronotal setae, and the three standard setae on the third interval of each elytron. The anterior supraoculars are lost often; the posterior, rarely, and only when the anterior ones are lost too (in New Guinea,

only in *Fortagonum bufo* and *Perigona rex*). Of the lateral pronotal setae, the median (anterior) pair are often lost; the posterior pair, rarely, unless the median pair are lost too (exceptions are *Lithagonum*, Part II, p. 176, and *Laevagonum subcitum*, Part II, p. 245), but both pairs have disappeared in some cases. Of the setae (seta-bearing punctures) of the third elytral intervals, sometimes only the anterior one on each elytron is lost, leaving the elytra together 4-punctate (*e. g.*, in *Iridagonum quadripunctum*, *Altagonum vallicola* and *grossulum*, and some *Maculagonum*); sometimes the anterior and middle ones are lost, leaving each third interval with only the posterior puncture and seta (*e. g.*, in some *Maculagonum*); sometimes these elytral setae disappear in some other order or are inconstant in single species (*e. g.*, in *Nebriagonum cephalum* and *transitum* and *Fortagonum fortellum*); and in some cases all these elytral punctures have been lost (*e. g.*, in *Altagonum exutum* and *fatuum*, *Nebriagonum percephalum*, and most *Laevagonum*). In the extreme case (only in *Fortagonum bufo*, on New Guinea), all these standard setae of head, pronotum, and elytra have been lost, leaving the insect without dorsal setae.

This is an incomplete survey of the extent of loss of setae by New Guinean Carabidae and of the diversity of setal patterns that has resulted. Most of the loss has occurred in mountain-living forms, but some loss of setae has occurred in lowland species too. Most of the loss has occurred in flightless (–winged) species, but some setae have sometimes been lost in winged species too. And most of the loss has occurred in Agonini, but this is probably because most mountain-living carabids in New Guinea are agonines; setae have been lost by mountain-living species of some other tribes in New Guinea too (*e. g.*, of Pterostichini, *Rhytiferonia*, *Analoma*, and some *Lesticus* have lost the setae of the third intervals, and of Perigonini, *Perigona rex* has lost the supraocular and lateral pronotal setae). In some cases loss of particular setae characterizes species or genera; in other cases setae vary individually in single populations (see especially *Prothorax* and *Elytra* of *Nebriagonum cephalum*, and *Notes* under *Fortagonum fortellum*). Loss of setae is usually bilaterally symmetric, although unsymmetric in occasional individuals. And in some cases, but apparently not usually, loss of different pairs of setae may be genetically correlated: *e. g.*, cases have been found (in the West Indies and Australia) in which single mutations eliminate both the anterior supraocular and the median-lateral pronotal setae, or both the median-lateral pronotal and anterior elytral setae (see [100]).

Why setae should be lost so often, especially by mountain-living Carabidae that have lost their wings, is difficult to say. The setae are probably tactile, and they may tend to be lost by beetles which have become relatively sluggish and which may have less need of tactile warnings than small, winged, active carabids do. It is also possible that presence of setae has some outright disadvantage—possibly as foci of infection, especially in humid situations in the cloud zone on mountains—which accelerates their loss when the need for them is lost. But loss of setae is something to be investigated by ecologists, behaviorists, and physiologists. I can only emphasize the fact of the loss. I cannot satisfactorily explain it.

[96] *Modification of legs and tarsi.* Evolutionary trends in modification of the legs and tarsi of New Guinean Carabidae especially on mountains surely exist. One trend is toward loss of lobes of the fourth hind-tarsal segments. These segments are often (not always) long-lobed in active lowland Carabidae, especially arboreal ones, and the lobes often are shorter or absent in less active, ground-living, montane forms. The legs may be shortened, too; perhaps this shortening is a secondary trend following wing atrophy in some cases. And the clothing of the lower sur-

face of the tarsi, and the accessory setae of the fifth tarsal segments, are often modified or partly lost. These details are so diverse among New Guinean Carabidae, and the evolutionary trends are so complex and so obscure, that I shall not attempt to say more about them now, but can only hope that persons who have the opportunity will consider them in more detail in the future.

[97] *Modification of ecology and behavior.* Besides trends in evolution (especially loss) of structures, trends in ecology and behavior probably occur among New Guinean Carabidae, especially on mountains. One trend is probably from waterside to mesophile habitats, especially to the floor of rain forest. Several lowland stocks have made this ecologic shift [91], and montane stocks have probably made it too. However, the montane Carabidae are so complexly interrelated and their habitats are so little known that I cannot give details.

Connected with the trend into mesophile habitats may be a trend toward reduced activity and possibly a trend toward increasingly nocturnal habits, at least in montane forests. I base this very tentative suggestion on what I saw of carabid behavior during the less than two weeks that I collected on the Bismarck Range [3].

Finally, there are presumably trends in density and distribution patterns of populations correlated with habitats and with altitude. At low altitudes in New Guinea, carabid populations probably tend to be sparse and patchy. This seems to be the case especially in the stable environment of the lowland rain forest, which suggests a trend toward patchy distributions there. Maintenance of wings by most lowland Carabidae in New Guinea is perhaps an adaptation to sparse, patchy distribution of populations [22]. However, with increasing altitude this trend is probably reversed. Species (populations) at higher altitudes often have very small total ranges (a single mountain-top, against the whole of New Guinea for many lowland species), but within their ranges these species presumably maintain relatively dense, relatively continuous populations, which can survive without flight. I think a trend like this, toward increasing concentration of individuals in populations at increasing altitudes, must occur, although (as far as I know) ecologists have not yet demonstrated it, at least not among Carabidae.

TABLE 18. NEW GUINEAN CARABIDAE WITH SMALL BUT ABRUPTLY PROMINENT EYES

(Agonini)
Notagonum reversum group (eyes abrupt in 3 of the 4 species; present part, Fig. 28)
Iridagonum (2 of the 7 species, *subfusum* and *vigil*)
Maculagonum (3 of the 13 species)
Gastragonum (1 of the 6 species, *laevisculptum*)
Idiagonum (all 6 species)
Montagonum (1 of the 8 species, *toxopeanum*)
Nebriagonum (some)
Fortagonum (some, especially *limum* and *distortum*; present part, Fig. 76)
(Non-agonines)
Dolichoctis distorta (Part III, Fig. 81)
Demetrida vigil (eyes abrupt but scarcely "popped"; Part III, Fig. 107)

[98] *Parallelism and convergence; development of elytral spines; color patterns.* Multiple parallelisms and/or convergences that have occurred among New Guinean Carabidae in atrophy of wings, in changes that follow wing atrophy, in loss of setae, and in modification of tarsi are described or implied in preceding pages. Some other structures or patterns which have been duplicated in the evolutions of different New Guinean Carabidae are worth noting. For example, the eyes have been reduced in many different stocks, especially in flightless ones, and, although the reduced eyes are usually flattened, they have become abnormally abruptly prominent ("popped") in about eight separate cases

TABLE 19. APPARENTLY SEPARATE STOCKS OF NEW GUINEAN CARABIDAE WITH ELYTRAL SPINES

(Agonini)
Tarsagonum latipes (Part II, Fig. 1)
Notagonum subrufum
" *spinulum*
" *sectum* (present part, Fig. 33)
Violagonum violaceum
Colpodes s. sloanei
" *helluo* (present part, Fig. 35)
" *rex*
" *antedens*
Plicagonum rugifrons (spines short, present only in some individuals)
Iridagonum quadripunctum (some individuals)
Altagonum tutum
" *cracens* (present part, Fig. 44)
" *avium* (present part, Fig. 45)
" *cheesmani, sororium* (present part, Figs. 39, 40)
" *scapha, regiscapha*
" *erugatum* (present part, Fig. 46)
" *stellaris* (present part, Fig. 43)
" *bigenum, subconicolle* (spines short; present part, Figs. 47, 48)
Potamagonum diaphanum (spines short, present only in some individuals; Part II, Fig. 8), etc.
Nebriagonum arboreum (spines short)

(Lieinini)
Omestes torta (spines short; Part III, Fig. 5)
Dicrochile acuta (spine short, present only in some individuals; Part III, Fig. 6)

(Lebiini)
Stenotelus spinosus (Part III, Fig. 44)
Catascopus latus (Part III, Fig. 60)
" *laevigatus*
" *sidus* (Part III, Fig. 61)
" *smaragdulus* (some individuals)
" *dobodura* (Part III, Fig. 62), *biroi*
" *wallacei*, etc. (Part III, Figs. 63, 64)
Pericalus figuratus (Part III, Fig. 65)
Dolichoctis distorta, aculeata group, *polita* group (Part III, Figs. 81–85)
Stricklandia pericalloides, lata (Part III, Fig. 86)
Demetrida tesselata (Part III, Fig. 98)
" *genicula* (Part III, Fig. 101)
" many other species (Part III, Figs. 103–109, VI, IX–XII)

(Odacanthini)
Clarencia quadridens (spines short; Part III, Fig. 128)
Dicraspeda bispinosa (some individuals; Part III, Fig. 129)
" *quadrispinosa, violacea*
Dobodura armata (Part III, Fig. 131)

among New Guinean Agonini (Table 18; see also Part II, p. 96) and in the lebiine *Dolichoctis distorta;* most of the carabids concerned are mountain-living, but *Dolichoctis distorta* is a lowland species. Convergence of body form, especially evolution of a strikingly fusiform body outline, has occurred in isolated species of at least four genera of Agonini (listed in Part II, p. 95). And ventral pubescence has been developed in probably ten independent cases in New Guinean Agonini (listed in Part II, pp. 100–101). Abruptly prominent eyes, fusiform body, and ventral pubescence are presumably adaptive, but I do not know their function among New Guinean Carabidae. However, something more can be said about development of elytral spines.

Most Carabidae have the apices of the elytra rounded or oblique or simply sinuate, but some have the sutural angles denticulate or the apices angulate, and some have evolved spines either as elongated denticles at the sutural angles or as acute prolongations of the apical angulations approximately opposite the ends of the third intervals, or at the outer-apical angles, or elsewhere. Elytral spines have apparently been evolved *independently* in at least 21 separate stocks of Agonini, 13 of Lebiini, two of Licinini, and four of Odacanthini listed in Table 19. The total number of cases in which elytral spines have evolved among New Guinean Carabidae is at least 40, and in most of these cases the spined forms have apparently originated on the island from spineless ancestors.

Elytral spines have evolved relatively often in Agonini and Lebiini but rarely in some other large tribes. For example, New Guinean Pterostichini are never spined, the nearest approach being in *Lesticus gracilis* (Part I, p. 524), in which the elytral apices are pointed or denticulate but not much produced. And New Guinean Harpalini, although numerous and dominant, are never spined, the nearest approach being in *Coleolissus papua* (Part III, p. 65, Fig. 26), in which the sutural angles are acutely denticulate. It is a question whether the tendency of some tribes to evolve spines more often than others reflects genetic differences or differences in ecology or behavior. Most or all of the spined Lebiini and some of the spined Agonini are arboreal, while no New Guinean Pterostichini or Harpalini are fully arboreal. However, some other spined Agonini (*Tarsagonum* at low altitudes and probably some of the mountain-living forms) are ground-living; the spined licinine *Omestes* lives on the ground in swamps; and *Dobodura* (one of the most strongly spined of all New Guinean Carabidae) lives among spray-drenched stones beside turbulent brooks. The correlation of spined elytra with arboreal habits is therefore not complete.

Elytral spines presumably tend to protect the insects against predators, including lizards and birds. It may be significant that, although spines have been developed in many different stocks of Agonini on New Guinea, there are no spined species among the very numerous Agonini on the Hawaiian Islands (E. C. Zimmerman, personal communication, 1968). Hawaii, of course, lacks native terrestrial predators (frogs and lizards), although some insectivorous birds are present. On the other hand spines are very rarely developed among Agonini or any other Carabidae on the West Indies, where frogs and insectivorous lizards are numerous.

Some convergence of elytral color patterns has occurred among New Guinean Carabidae. Most striking is development of patterns formed by short longitudinal pale lines arranged in three transverse series on a dark ground. These patterns occur in some (not all) species of small lebiines of the not–directly–related genera *Minuthodes*, *Coptodera*, and *Agonochila* (cf. Part III, Figs. 48, 68, 72, etc.). The pertinent species of the first two of these genera occur on the trunks and branches of trees, and the *Agonochila* may do so too, although I do not know the habits of this genus in New Guinea. This convergence of patterns may be mimetic (see below). Also possibly mimetic may be the striking coloration (red head and prothorax, blue elytra) of the rare lebiine *Phloeocarabus euplenes* (Part III, p. 184), which differs strikingly from other members of its genus but resembles in color the relatively common agonine *Euplenes apicalis.* A pattern of fine light and dark speckling has evolved convergently in *Maculagonum* (Agonini) and in certain *Demetrida* (Lebiini), *e. g.*, *D. pallens* (Part III, Pl. 1, Fig. II). This pattern may be not mimetic but cryptic in places where light and shade are finely divided, for example in grass. A different pattern of convergence occurs in *Chlaenius*, of which six species that normally have pale markings on the elytra elsewhere in their extensive ranges are losing or have lost the markings in New Guinea (see Part III, p. 22, last paragraph of first column). These species live in somewhat diverse habitats (although all on the ground, of course), and I think this loss of elytral markings is probably not mimetic but may be the result of ecologic factors acting similarly on the several species. Convergence of an elytral color pattern consisting of a conspicuous pale square mark before the apex of the elytra in some *Trichotichnus* (Harpalini), *e. g.*, *T. guttula* (Part III, p. 57), and in some *individuals* of *Altagonum grossulum* or *grossuloides* (Agonini) (see present *Taxonomic supplement*) may be due to parallel mutations and may have no direct adaptive significance.

[99] *Mimicry.* The parallelisms or convergences discussed in preceding paragraphs are of several sorts. Some, including wing atrophy, the secondary structural changes that often follow it, and loss of setae are probably at least in part adaptations to complex new environmental factors encountered especially at higher altitudes. The development of spines may be directly protective. Speckled coloration may be cryptic in special situations. Loss of color patterns by *Chlaenius* may be a selective response to a relatively simple (but unknown) climatic factor. Convergence in some details of markings may be due to parallel mutation. And parallelism or convergence in color pattern of certain small Lebiini and of *Phloeocarabus euplenes* may be mimetic.

Mimicry has recently been usefully rediscussed by Wickler (1968). It is surely very common among insects in the tropics. Nevertheless, it is not always easy to decide whether particular resemblances are mimetic or not. After seeing many New Guinean Carabidae alive (mimicry is partly a matter of behavior of living individuals), I doubt if mimicry is common among them, but I can suggest the following possible cases for consideration in the future. Mimicry may be involved not only in the convergence of color patterns of the small, tree-trunk-living Lebiini referred to above, but also in the evolution of form and color of some *Demetrida*, perhaps most likely in the similarity of *D. imitatrix* to the very common, spined (and perhaps for other reasons protected) *Violagonum violaceum* (see Part III, pp. 176–177). The antlike form of *Colasidia* (present part, *Tax. suppl.*) may also be mimetic. (And the antlike tiger beetle *Tricondyla* may derive some advantage from its similarity to a large ant, although I am not sure that any ants comparable to *Tricondyla* in size and behavior occur in New Guinea, and although *Tricondyla* itself is a formidable insect.)

[100] *Mutation and dimorphism.* Mutations resulting in Mendelian dimorphism have apparently occurred among New Guinean Carabidae. Known cases are worth listing and describing, for mutation and dimorphism sometimes mark the beginning of important evolutionary processes and sometimes affect characters supposedly important in taxonomy.

Mutation from a long- to a short-winged condition, and resultant dimorphism of wings, have been discussed in preceding sections [21–23]. Change from a long- to a short-winged condition probably usually or always begins (among Carabidae) with mutation, and dimorphism of wings is common. Lowland New Guinean Carabidae known to have dimorphic wings are indicated in Table 3, section [21]. Although wings have atrophied much more often at high than at low altitudes, actual dimorphism is rare at high altitudes in New Guinea. The only Carabidae known to be wing-dimorphic at high altitudes on New Guinea are *Trichotichnus nigricans* (fully winged at low altitudes but dimorphic on the Bismarck Range), *T. altus* (a mountain-living species which may be fully winged at some localities but is dimorphic at others), and *Gastragonum terrestre* (which is dimorphic on the Bismarck Range). Even most genera of Carabidae on the high mountains of New Guinea are uniformly long-winged or uniformly short-winged. The only known exceptions are *Gastragonum*, a natural genus which includes +w, ±w, and −w species, all living at considerable altitudes, and *Notagonum*, a "genus of convenience" of many winged species but including the "*reversum* group" (present part, *Tax. suppl.*), a natural group of four mountain-living species of which three are long- and one short-winged. This general situation suggests that, while some Carabidae at low altitudes in New Guinea are still unstable as to wings, with mutations continually occurring and dimorphism becoming established at least for short periods, the situation is more stable at higher altitudes.

Mutations presumably continue to occur at high altitudes too, but the wings in each group have apparently become adapted to the way of life of that group and are usually no longer liable to establishment of dimorphism and further evolutionary change. This is to suggest what may well be true, that some carabid populations at low altitudes in New Guinea are relatively unstable and liable to change or overturn, while many of the alticoline groups are more stable, more exactly adapted to special habitats, and less liable to significant changes or to overturns.

Occurrence of setae is known to be dimorphic in one species of carabid on New Guinea. It is *Perigona astrolabica* (Part III, p. 9), in which the posterior-lateral pronotal setae are present or absent. The absence is presumably due to a single mutation inherited in Mendelian fashion. (Similar mutations may have produced the same pattern of reduction of pronotal setae in *Lithagonum* (Part II, p. 176) and *Laevagonum subcitum* (Part II, p. 245).) Strict dimorphism of setae is not known in any other Carabidae on New Guinea. (In some species especially of *Nebriagonum* occurrence of setae varies erratically but is not simply dimorphic.) However, patterns of setae do vary strikingly from species to species in some genera, and it seems likely that the variations begin by mutation and that the mutations are followed by seta-dimorphism at least for short periods.

Outside New Guinea, seta-dimorphism has been found in a few Carabidae. In the lebiine *Phloeoxena deälata* Darlington (1937: 136) of Cuba, the anterior supra-ocular setae and median-lateral pronotal setae are apparently inherited as a group, these four setae being either all present or all absent in all of 33 individuals from a single mountain top. This dimorphism presumably originated by a single mutation. A similar mutation may have produced the same pattern of seta-loss in "*Altagonum*" *bigenum* (present part, *Tax. suppl.*). In *Notagonum macleayi* (Sloane) of North Queensland, the anterior-lateral (=median-lateral) pronotal setae and the anterior seta-bearing punctures of the third elytral intervals are apparently inherited as a group: all four of these setae are present or all absent in all of 48 individuals, with one partial exception (see Darlington, 1963: 4 for further details). In this case, too, absence of the setae is probably due to one Mendelian mutation. Homologous mutations may have produced the same pattern of loss of setae found in New Guinea in *Altagonum vallicola* and *grossulum* and *Iridagonum quadripunctum*.

Dimorphism of elytral color pattern apparently occurs in *Minuthodes sexualis* and perhaps in *M. papuana* (Part III, pp. 99, 97), in *Demetrida diversa* (Part III, p. 172) and perhaps other species of *Demetrida*, and possibly but less obviously in some other New Guinean carabids including perhaps *Tachys acuticollis* (see present part, *Tax. suppl.*).

In summary, mutations from a long- to a short-winged condition probably occur commonly among New Guinean Carabidae, and wing dimorphism, presumably following mutation, has been found in some species, mostly lowland forms. Mutations eliminating setae are probably common too and are probably diverse, producing many different patterns of setal reduction, although known cases of strict dimorphism of setae are few. And mutations are probably continually affecting a variety of other characters, including color patterns, although they are hard to detect in most cases.

State of wings and patterns of setae are sometimes important taxonomic characters. If mutations affect them, as they do, they probably affect many other characters used by taxonomists. It is therefore of practical taxonomic importance as well as of theoretical evolutionary interest to detect occurrences of mutation and dimorphism in nature. Their occasional occurence does not spoil the taxonomic usefulness of the

characters concerned, provided proper allowance is made for them (cf. *Nature of taxonomic characters* [12]).

Variation which is presumably primarily genetic, beginning with mutation and passing through stages of dimorphism (although the dimorphism may be obscure or brief) occurs even in characters supposedly of generic and tribal importance. For example, presence of a subapical fold of the elytral margin in Pterostichini and its absence in Agonini distinguish most members of these tribes. However, the fold is variable or lost in a few pterostichines. It is present or absent in different individuals of *Analoma fortis* (Part I, p. 539); present in *Lesticus ambulator* but absent in the presumably related *L. toxopei;* and variable in the *Loxandrus-Homalonesiota-Nebrioferonia-Haploferonia* group of genera (Part I, pp. 547ff; present part, *Tax. suppl.*).

Number of supraocular setae—whether one or two on each side—is a useful and, with proper allowance for exceptions, natural character for distinguishing some tribes of Carabidae. The anterior supraoculars are often lost, sometimes evidently by mutation (see above), and the posterior setae then usually remain, usually near or diagonally behind the posterior corners of the eyes. To the experienced carabid taxonomist this position of the posterior supraocular setae indicates that the species in question are derived from and belong in tribes which normally have two pairs of supraoculars. (Of course this guide fails in the cases, very few in New Guinea, in which both pairs of supraocular setae have been lost.) However, in the special case of *Miscelus* (Part III, p. 91, Figs. 168, 169) the supraocular setae behave differently. No one species of this genus is dimorphic, so far as I know, but different species that are otherwise extremely similar have either one or two setae over each eye, and when only one setae is present, it is in median position, not in the normal position of the posterior setae. *Miscelus* is a taxonomically isolated carabid, placed sometimes in the tribe Lebiini and sometimes in a tribe of its own. Regardless of its evolutionary history (which I do not know), it is at least a striking example of an exception, which has probably originated by mutation, in a character ordinarily of tribal value.

Modification of the clothing of the male tarsi in *Lyter* (Part III, p. 63) is another example of an exception to a character usually of broad taxonomic significance. In most Harpalini the males have the lower surface of the front and often also of the middle tarsi clothed either with two rows of broad scales or with a dense pad of very narrow scales; this difference is the basis for distinguishing major subtribes of Harpalini (Part III, p. 40, in *Key*). In *Lyter,* however, the male tarsi are loosely clothed with several irregular rows of moderately slender scales. This condition is intermediate between the 2-seriate and densely padded types of tarsal clothing. *Lyter* is probably derived from an ancestor, perhaps a *Trichotichnus,* with two rows of male tarsal scales. No transitional conditions have been found in the numerous species of *Trichotichnus* that I have seen from New Guinea and the Orient; the change from 2-seriate to multiseriate tarsal clothing may therefore have been by mutation. And abrupt, perhaps mutational loss of the scales of the male middle (not front) tarsi is suggested in *Trichotichnus seminus* and *Harpaloxenus fortis* (Part III, pp. 52, 60), in both of which middle-tarsal scales are absent although present in apparently closely related species on New Guinea. (Mutation should be suspected, too, in loss of male tarsal clothing by various other Harpalini outside New Guinea.)

Mutation is to be suspected and dimorphism looked for in other taxonomic characters that vary abruptly. Striking differences in presence or absence of lobes on the fourth tarsal segments of different species of *Notagonum* (Part II, pp. 127ff, especially p. 128) and different species of *Dicraspeda* (Part III, pp. 210ff) may be

in part mutational. The difference between the pectinate claws of *Desera* and the simple claws of *Drypta* (Part III, pp. 216ff, especially p. 218) may be mutational. And abrupt differences in some details of the male genitalia may be mutational although, because I have made little use of genitalic characters in the present work, I cannot give examples from New Guinean Carabidae. All these cases need further study based on or following more thorough, third-stage taxonomic treatment. For the moment I can only do what I have had to do elsewhere in preceding pages: point out that important problems exist, although I cannot solve them.

TAXONOMIC SECTION

[101] *Tribal classifications.* I should like to have included here a classification and key to the tribes of Carabidae that occur in New Guinea, but I have decided against it. To make such a classification based on New Guinean Carabidae would be laborious, and would not be a very important contribution to carabid classification, since the New Guinean fauna is very limited. In fact it includes representatives of only about one-third of existing carabid tribes [18]. For practical identification of tribes of New Guinean carabids, the best key is probably Andrewes' (1929: 43–46), which is based on tropical Asiatic forms and which includes, I think, all tribes that are represented in New Guinea. This key is only four pages long, and interested persons can easily secure copies of it. Sloane's (1923) "Classification of the family Carabidae" is concerned with the Australian forms, and can be tried for New Guinean ones when Andrewes' table fails. Ball's (1960) classification of Carabidae includes many improvements but is concerned primarily with the North American fauna and therefore omits some tribes that are found in New Guinea. Jeannel's (1941–1942) classification (in *Faune de France*, Part I, pp. 9–10, 77–88, supplemented by footnotes scattered throughout the work) is important and should be studied by all persons interested in tribal classifications of Carabidae, but it seems to me that it splits families, tribes, and lower groups far beyond practical usefulness. And Basilewsky (1953), in keys to higher categories of Carabidae represented in Africa and Madagascar, follows Jeannel's classification in a general way but makes some changes.

TAXONOMIC SUPPLEMENT

This supplement consists of important new records and new species of Carabidae received from New Guinea too late to be included in preceding parts of my work. Many tribes, genera, and species about which I have nothing important to add are omitted. For some other tribes and genera only an indication of additional material available for future study is given, usually with a list of the species that have been found at Wau, which has become a locality of special importance. But in still other groups, notably some mountain-living Pterostichini and Agonini, new material necessitates complete revisions of genera, with new keys and complete lists of species. References are usually limited to Parts I, II, and III of the present work, where additional references will usually be found.

Subfamily CICINDELINAE

Darlington 1962, Part I, p. 333.

See Rivalier (1950–1963), "Demembrement du genre *Cicindela* L.," especially parts IV (1961), "Faune indo-malaise," and V (1963), "Faune australienne." This is an important contribution to understanding of the *Cicindela* (*sensu lato*) of New Guinea and adjacent areas. I have not myself anything further to say about New Guinean tiger beetles.

Subfamily CARABINAE
Tribe OZAENINI
Genus *PSEUDOZAENA* Castelnau

Pseudozaena orientalis opaca (Chaudoir)

Darlington 1962, Part I, p. 352.

Additional material. Seventy-two, from numerous localities, including 22 from Wau, 1200 m (none higher); and 4, **Waigeo Is.,** Camp Nok, 2500 ft. (*c.* 760 m), Apr. 1938 (Cheesman).

Tribe SCARITINI
Genus *GEOSCAPTUS* Chaudoir

Geoscaptus cacus (Macleay)

Darlington 1962, Part I, p. 356.

Additional material. **N-E. N. G.**: 3, Main River, Sepik, Feb. 1965 (Hornabrook). **West N. G.**: 1, Ifar, Cyclops Mts., 300–500 m, June 23–25,1962 (Sedlacek).

Genus *CLIVINA* Latreille

Darlington 1962, Part I, p. 358.

Notes. Of this genus, 218 additional specimens have been received from New Guinea. They include the following species from Wau and vicinity:

fessa Darlington: 1200 m (many), 1500 m (1)
brandti Darlington: 1200 m (1)
szekessyi Kult: 1200 m (2)

Besides these, *tripuncta* Darlington and *subfusa* Darlington might be expected to occur at Wau but have not yet been found there.

Additional important records from other parts of New Guinea, and 2 new species, follow. Besides the additional material identified (but not all listed), I have seen 5 specimens which I cannot identify satisfactorily and which I have labeled "*Clivina* spp." They are all returned to the Bishop Museum.

Clivina wallacei Putzeys

Darlington 1962, Part I, p. 365.

Additional material. **Papua**: 3, Palmer R. at Black R., June 7–14, July 23–31, 1936 (Archbold Exp., AMNH).

Notes. Putzeys' original material may have come partly from (western) New Guinea (see discussion in my Part I, cited above), but the present specimens are the first surely recorded from the island. Two of the specimens have the labrum 6-setose, one 5-setose, but I am confident they are all *wallacei.* Variation in number of labral setae occurs in Philippine individuals too.

Clivina kulti Darlington

Darlington 1962, Part I, p. 366.

Additional material. **Papua**: 1, Popondetta, 60 m, Sept. 1–4, 1963 (Sedlacek).

Notes. Previously known only from the types from Aitape, **N-E. N. G.**

Clivina deleta Darlington

Darlington 1962, Part I, p. 375.

Additional material. **Papua**: 1, Mt. Lamington, 500 m, June 1966 (F. Shanahan, C. E. Lippert, Bishop Mus.). **N-E. N. G.**: 1, Siaute, Torricelli Mts., sea level, Nov. 9–17, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Waris S of Hollandia, 450–500 m, Aug. 1–7, 1959 (C. T. Maa, Bishop Mus.), m. v. (mercury vapor) light trap; 1, Archbold L., Central Mts., 760 m, Nov. 26–Dec. 3, 1961 (S. & L. Quate, Bishop Mus.).

Notes. Previously known only from the types from Dobodura, **Papua.**

Clivina basalis Chaudoir

Darlington 1962, Part I, p. 383.

Additional material. **Papua**: 2, L. Daviumbu, Fly R., Aug. 19–30, 1936 (Archbold Exp., AMNH). **N-E. N. G.**: 10 Aiyura, 1600 m, June 6, 1966 (Gressitt), light trap; 1, Kainantu, 1650 m, Oct. 20–26, 1959 (Maa, Bishop Mus.), m. v. light trap.

Notes. Although *basalis* occurs in **Java, Celebes**, and **Australia** as well as New Guinea, on the latter it has been found only in the eastern part of the island. Most New Guinean specimens have the elytra red anteriorly and black posteriorly. However, the 2 from L. Daviumbu have the elytra red with the black area reduced to 2 large postmedian maculae as in specimens from tropical Australia, suggesting that the Fly R. population may be independently derived from Australia.

Clivina fessa Darlington

Darlington 1962, Part I, p. 388.

Additional material. Seventy-four, from all 3 political divisions of New Guinea; a few at low altitudes but chiefly in the mountains, including 58 specimens from Wau and vicinity (most at 1200, 1 at 1500 m), some taken at light.

Notes. I now think *fessa* is closely related to *subfusa* Darlington (Part I, p. 384), which is another New Guinean mountain-living species. These 2 species are somewhat similar in form, and both have the middle tibia with spur very near apex. However, *fessa* differs from *subfusa* in having eyes larger, elytral margins usually subcrenulate behind humeri, and mid-tibial spurs a little longer.

Clivina australasiae group

Darlington 1962, Part I, pp. 361, 380–397.

Notes. Specific characters in this group are poorly understood and perhaps variable. Additional material (included in total noted under genus) has been identified according to key characters, but I have not attempted further study of it except to record the second known specimen assignable to *C. csikii* Kult and to describe 2 obviously distinct new species.

Clivina csikii Kult

Darlington 1962, Part I, pp. 362, 390.

Additional material. **West N. G.**: 1, Hollandia area, W Sentani, Cyclops Mts., 150–250 m, June 18, 1959 (Gressitt & Maa), in Malaise trap over stream.

Notes. This specimen agrees very well with my redescription of the type, which is from Madang, **N-E. N. G.** The species may well be distinct. It is distinguished, among other similar ones in New Guinea, by relatively slender form and small size (*c.* 5 mm).

Clivina kubor n. sp.

Description. Form as figured (Fig. 17), large, with oval-elongate elytra; black, appendages dark reddish; moderately shining, reticulate microsculpture irregular on front and pronotum and faint on elytra, but surface sparsely irregularly punctulate. *Head* 0.66 width prothorax; eyes rather small, genae *c.* long as eyes, arcuate; antennae

rather long (in genus), middle segments *c.* long as wide; mandibles rather short; labrum 7-setose; clypeus weakly evenly emarginate, with wings not separated by notches; front irregularly convex, frontal sulci sharply defined, nearly straight, converging anteriorly, reaching neck posteriorly; neck constriction scarcely impressed; supraocular convexities separated from preocular plates by oblique impressions. *Prothorax* narrowed anteriorly; width/length 1.03; disc convex, middle line fine, anterior transverse impression deep. *Elytra* elongate-oval, narrowed anteriorly as well as posteriorly; width elytra/prothorax 1.25; humeri not dentate; striae deep anteriorly, shallower posteriorly, faintly punctulate; 3 striae free at base; intervals strongly convex anteriorly, 7th briefly finely carinate at base, 3rd with 4 or more punctures on outer edge (4 on left, 6 on right elytron). *Inner wings* evidently atrophied but not examined in the single specimen. *Lower surface*: proepisterna weakly punctate inwardly; last ventral weakly transversely wrinkled but not punctate, with 2 setae on each side widely separated. *Legs*: front femur moderate; front tibia 2-dentate above a long curved spur; middle tibia with rather short spur on outer edge near apex. *Measurements*: length *c.* 9 mm; width 2.8 mm.

Type. Holotype (sex not determined) (MCZ, Type No. 31806) from "Sarua Kup," Kubor Rge., **N-E. N. G.**, Oct. 31, 1965 (altitude and collector not given, but altitude probably high, and specimen received from Dept. Agr. Port Moresby); the type is unique.

Notes. This new species is comparable in form with *C. toxopei* Darlington (Part I, p. 363) but is much smaller, with smooth rather than wrinkled head, and different in many other ways. The similarity in form is presumably convergent, a result of loss of wings and resulting changes of form. The new species is in fact not related to *toxopei* but is apparently a derivative of the *australasiae* group (see Darlington, Part I, p. 361, in key). It is perhaps most closely related to and possibly derived from *C. subfusa* Darlington (Part I, p. 384), which it resembles in form of spur of middle tibia, but the new species is larger, with more oval and more deeply striate elytra, and it differs in other details. Also, *subfusa* is winged, while *kubor* obviously has the wings atrophied. It is likely that the present new species will prove to live at higher altitudes than *subfusa*, although the latter is a mountain-living species.

Clivina alternans n. sp.

Description. Form as figured (Fig. 18); slightly depressed; irregularly rufous; rather dull, much of upper surface irregularly punctulate, elytra microreticulate. *Head* 0.67 and 0.66 width prothorax; eyes rather small, genae arcuate-subtruncate, meeting neck abruptly; antennae moderate, middle segments almost long as wide; mandibles average; labrum 7-setose; clypeus truncate (very weakly arcuate-emarginate) with wings not separated by notches; supraocular convexities separated from preocular plates by deep impressions; front flat, ± punctate; frontal sulci slightly sinuous, reaching posteriorly nearly to neck; neck not impressed at middle. *Prothorax*: width/length 1.08 and 1.05; disc moderately convex with fine middle line and slightly deeper transverse impression. *Elytra*: width elytra/prothorax 1.21 and 1.19; humeri not much narrowed, not dentate; margin scalloped (much interrupted) almost to apex; 3 striae free at base; striae well impressed, faintly punctulate; intervals alternating in width, odd intervals (especially 3 and 5) wider than even intervals; 6th and 7th finely carinate at base, 3rd 4-punctate. *Inner wings* fully developed. *Lower surface*, especially proepisterna and abdomen, roughened. *Legs*: front femora moderate; front tibiae 2-dentate above the apical process (a 3rd tooth indicated by angulation and seta); middle tibiae with moderate spur *c.* 1/4 from apex. *Measurements*: length 5.7–5.9 mm; width 1.8–1.9 mm.

Types. Holotype (sex not determined) (Bishop Mus.) from Eliptamin Valley,

N-E. N. G., 1200–1350 m, July 1–15, 1959 (W. W. Brandt); 1 paratype (Bishop Mus.), Mobitei, Torricelli Mts., N-E. N. G., 750 m, Mar. 5–15, 1959 (W. W. Brandt); 1 paratype (MCZ, Type No. 31807), Bokodini, 40 km N of Baliem Vy., **West N. G.**, *c.* 1300 m, Nov. 16–23, 1961 (S. & L. Quate), light trap; 1 paratype (Bishop Mus.), Kebar Vy., W of Manokwari, West N. G., Vogelkop, 550 m, Jan. 4–31, 1962 (S. & L. Quate), taken in Malaise trap.

Notes. In my key to *Clivina* of New Guinea (Part I, pp. 359–362) this runs to the second part of couplet 14 (the *australasiae* group), but differs from all species named thereunder in having elytral intervals alternating in width. Otherwise possibly most similar to (but not necessarily related to) *fessa* Darlington (Part 1, p. 388) but differing in alternation of intervals. The flattening of the front, scalloping of the elytral margins (indicated only behind humeri in *fessa*), and rugose lower surface of *alternans* (partly rugose also in *fessa*) are also distinctive characters. It seems likely that this species is widely distributed at moderate altitudes in the lower mountains of New Guinea.

Subfamily HARPALINAE
Tribe BEMBIDIINI
Genus *TACHYS* Stephens

Darlington 1962, Part I, p. 400.

Notes. Additional specimens of *Tachys* received from New Guinea total 456. Most are from light-trap material, and many are therefore damaged or matted with scales of Lepidoptera. These specimens are difficult to study; some I have simply labeled, "Not in condition to determine." Nevertheless this material was well worth collecting and submitting. I have been able to pick out from it important new records of poorly known species as well as several new species.

The following 11 species of *Tachys* have been found at or near Wau:

T. fasciatus (Motschulsky), at 1200 m (1 specimen)
T. ochrioides Darlington, at 1200 m (2)
T. reticuloides Darlington, at up to 1200 m (only 2 at this altitude)
T. reticulatus Andrewes, at 900 m (6)
T. pictus Andrewes, subspecies, altitudes from 900 to 1800 m (15 in all)
T. bembidiiformis Jordan, at 1200 m (1)
T. erotyloides Andrewes, at 1100, 1500 m (3)
T. klugi Nietner, at 1200 m (1)
T. fumicatus Motschulsky, at 1200 m (1)
T. umbrosus Motschulsky, at 1050, 1100, 1150, 1200 m (6)
T. acuticollis Putzeys, at 1000, 1050, 1100 m (4)

Of these 11 species from the vicinity of Wau, *reticuloides, reticulatus, pictus* and *erotyloides* usually occur (at other localities) by running water; *umbrosus* and *acuticollis*, on or under bark; the others, on the ground in various wet places. The small number of specimens of most species suggests that additional *Tachys* are still to be found at Wau.

The following additional records and new species are all that seem to be worth recording in detail from the new material.

Tachys apex Darlington

Darlington 1962, Part I, p. 414.

Additional material. **West N. G.**: 1, Waris, S of Hollandia, 450–500 m, Aug 16–23, 1959 (T. C. Maa, Bishop Mus.); 1, Japen Is., SSE Sumberbaba, Dawar R., Oct. 24, 1962 (H. Holtmann, Bishop Mus.), in jungle.

Notes. Previously known only from the types from Nadzab, **N-E. N. G.**

Tachys brachys Andrewes

Darlington 1962, Part I, p. 433.

Additional material. **Papua**: 1, Bisiatabu, Port Moresby (W. N. Lock, South Australian Mus.).

Notes. This individual, like the 3 previously recorded from New Guinea, is fully winged.

Tachys ceylanicus (Nietner)

Darlington 1962, Part I, p. 446.

Additional material. **West N. G.:** 1, Nabire, S of Geelvink Bay, 10–40 m, Oct. 7, 1962 (H. Hoffmann, Bishop Mus.), "jungle."

Notes. Of this species, which is very common from **South Asia** to the **Moluccas**, only one specimen has been found heretofore in New Guinea (at Hollandia).

Tachys par Darlington

Darlington 1962, Part I, p. 452.

Additional material. **West N. G.**: 6, Bodem (11 km SE of Oerberfaren, 100 m), July 7–17, 1959 (T. C. Maa, Bishop Mus.); 1, River Tor (mouth), 4 km E of Hol Maffen, July 2–5, 1959 (T. C. Maa, Bishop Mus.), m. v. light trap.

Notes. The unique type is from Maffin Bay, West N. G.

Tachys klugi (Nietner)

Klugii Nietner 1858, Ann. Mag. Nat. Hist., (3) 2: 423 (*Bembidium*).
klugi Andrewes 1925, Ann. Mus. Civ. Genoa, 51: 401, 414, Pl. 3, fig. 6.

Description (for recognition only). Very stout and convex member of *politus* group; black or brassy, elytra usually each with small pale spot near apex; shining, reticulate microsculpture virtually absent; all elytral striae present, deeply impressed, punctulate, 1st entire, others abbreviated anteriorly and posteriorly; length (outside N. G.) *c.* 2.7–3.0 mm.

Types. From Ceylon; in Berlin Zool. Mus. (not seen).

Occurrence in New Guinea. **N-E. N. G.**: 1, Wau, Morobe Dist., 1200 m, Jan. 5–10, 1962 (Sedlacek), in Malaise trap.

Notes. This common Oriental species has been known from **India**, etc., north to **Japan** and east and south across the islands to the **Philippines** and to the **Moluccas** (specimens from Morotai Is. in MCZ), but the present record is the first from New Guinea.

Tachys convexus (Macleay)

convexum Macleay 1871, Trans. Ent. Soc. New South Wales, 2: 115 (*Bembidium*).
convexus Darlington 1963, Psyche, 70: 29.

Description (for recognition only). Member of *politus* group; very convex; 4-maculate; prothorax subglobose with posterior angles reduced to minute tubercles; basal transverse sulcus of pronotum 3-foveate at middle; elytra 1-striate; length *c.* 2.4 mm.

Type. From Gayndah, Queensland, **Australia**; presumably in Macleay Mus., Sydney (not seen).

Occurrence in New Guinea. **Papua**: 1, Oriomo River, 6 m, Feb. 12, 1964 ("H. C.," Bishop Mus.).

Notes. *T. convexus* is a common East and North Australian species which ranges north to the tip of Cape York (Darlington, 1963: 31) and (according to the present record, the first from the island) occurs also on the southern edge of New Guinea.

The form of this species, especially the almost globose prothorax with posterior angles reduced to small tubercles, is very different from that of any other *Tachys* known from New Guinea.

Tachys parasenarius n. sp.

Description. With characters of genus and of *politus* group (Darlington 1962, Part I, p. 435); form slightly more slender than average, normally convex; slightly reddish testaceous with suture and elytral margins darker, the dark areas not sharply defined; shining, reticulate microsculpture faint or absent. *Head* 0.78 and 0.79 width prothorax, without unusual characters. *Prothorax*: width/length 1.40 and 1.45; base/apex 1.14 and 1.13; sides broadly arcuate, broadly moderately sinuate to *c.* right well defined basal angles; disc normal; transverse basal sulcus well defined, subpunctate, interrupted at middle and with median fovea. *Elytra*: width elytra/prothorax 1.45 and 1.40; sides subparallel to behind middle, not noticeably fusiform, with humeri nor-

mally rounded; each elytron with 6 impressed striae, 1st entire, others abbreviated at both ends, shorter externally, 7th stria faintly indicated, 8th (submarginal) stria deep, entire, not bowed away from margin. *Measurements*: length *c.* 2.3 mm; width 0.9–1.0 mm.

Types. Holotype ♂ (Bishop Mus.) and 2 paratypes (♂ in MCZ, Type No. 31808, ♀ in Bishop Mus.) all from Waris, S of Hollandia, **West N. G.**, 450–500 m, Aug. 16–23, 1959 (T. C. Maa), at light.

Measured specimens. The ♂ holotype and ♀ paratype.

Notes. In my key to *Tachys* of the *politus* group of New Guinea (1962, Part I, pp. 437–439), this would run to couplet 26 but would fit neither species there named, being much more slender than *bembidiiformis* and differently colored; and smaller, more shining, and relatively larger-headed than *senarius*. The new species may be related to *senarius* and, like the latter, probably lives beside running water, to judge from the long series of other stream-side species collected with it.

Tachys tatei n. sp.

Description. With characters of genus and of *politus* group (Darlington 1962, Part I, p. 435); form *c.* average except less convex than usual; piceous, head and prothorax slightly reddish, elytra more distinctly red at apex, legs pale, antennae dark except pale at base; rather shining, reticulate microsculpture distinct and isodiametric on front (less distinct in ♂), less distinct and somewhat irregular but apparently *c.* isodiametric on pronotum, very fine and strongly transverse on elytra, which are subiridescent. *Head* 0.82 and 0.81 width prothorax; without unusual characters. *Prothorax*: width/length 1.51 and 1.52; base/apex 1.09 and 1.14; sides broadly arcuate, broadly sinuate before *c.* right well formed basal angles; disc normal with basal transverse sulcus moderately impressed, not distinctly punctate, more or less interrupted at middle and with median fovea. *Elytra*: width elytra/prothorax 1.47 and 1.50; humeri rounded; sides subparallel to behind middle; each elytron with 4 or more well-impressed striae (number that seem well impressed depends partly on lighting and angle of view, but is somewhat variable), 1st stria entire, others abbreviated, progressively shorter and less impressed externally, but trace even of 7th stria present in some individuals, 8th stria entire but not bowed away from margin. *Measurements*: length 2.8–3.3 mm; width 1.2–1.4 mm.

Types. Holotype ♂ (AMNH) and 6 ♀♀ paratypes; (2 in MCZ, Type No. 31809) all from Peria Creek, Kwagira River, **Papua**, 50 m, "[camp] No. 7," Aug 14–Sept. 6, 1953 (Geoffrey M. Tate); all specimens in poor condition, but most good enough to show characters.

Measured specimens. The ♂ holotype and one ♀ paratype.

Notes. How this new species would run in my key to *Tachys* of the *politus* group of New Guinea (1962, Part I, pp. 437–439) would depend on how many striae were considered present and impressed. If it were considered 4- or 5-striate, it would probably run to *borneensis*, but the outer elytral striae are much more impressed than in *borneensis*, and the coloration is much darker; nevertheless, the new species may be a relative of *borneensis*. If the elytron were considered 6-striate, the new species would probably run to *senarius*, but it differs from *senarius* and also from *parasenarius* (above) in darker color and in details of form.

Tachys tor n. sp.

Description. With characters of *Tachys* and *politus* group (Darlington 1962, Part I, p. 435); form about average in group and of average convexity; head and prothorax reddish testaceous, elytra brownish piceous, each with large macula covering most of apical third of elytral length testaceous, appendages testaceous with antennae browner except at base; rather dull, reticulate microsculpture distinct, isodiametric on front and pronotum, somewhat transverse

on elytra. *Head* 0.72 and 0.74 width prothorax; without unusual characters. *Prothorax*: width/length 1.55 and 1.41 (width more variable than usual); base/apex 1.27 and 1.24; sides broadly arcuate, moderately sinuate before right or acute well-defined posterior angles; disc normal, basal transverse sulcus rather shallow, subpunctate, interrupted and with fovea at middle. *Elytra*: width elytra/prothorax 1.43 and 1.48; widest behind humeri, then slightly narrowed but not strongly fusiform; humeri rounded; elytra each 7-striate, 1st stria entire, others abbreviated at both ends and progressively shorter externally and also less impressed externally, 7th being an irregular lightly impressed line, 8th (submarginal) stria entire, not much bowed away from margin. *Measurements*: length 2.3–2.6 mm; width 1.0–1.1 mm.

Types. Holotype ♂ (Bishop Mus.) and 3 paratypes (♂ ♀ in MCZ, Type No. 31810, ♀ in Bishop Mus.) all from River Tor (mouth), 4 km E of Hol Maffen, **West N. G.**, July 2–5, 1959 (T. C. Maa), in light trap (2) and m. v. light trap (2).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This new species does not fit into my key to species of *Tachys* of the *politus* group of New Guinea (1962, Part I, pp. 437–439), because 7-striate elytra are not found in any *Tachys* previously known from the island (except *klugi*, not in the key but recorded in the present paper—the present new species is much more slender and not related to *klugi*). Actually, the new species is probably related to *senarius* and also to *parasenarius* (described above) but differs in color (the 2 species just named are testaceous with at most rather poorly defined elytral markings) and in having the 7th striae better developed, although still weak.

Tachys fumicatus Motschulsky

Darlington 1962, Part I, p. 469.

Additional material. New material includes **West N. G.**: 2, Kebar Valley, W of Manokwari, Vogelkop, 550 m, Jan. 4–31, 1962 (S. & L. Quate, Bishop Mus.), light trap; 1, Nabire, S of Geelvink Bay, 20–50 m, July 9, 1962 (H. Holtmann, Bishop Mus.).

Notes. These 3 specimens have elytra entirely unspotted; previously known New Guinean individuals are all 2- or 4-spotted, as described in detail by me in 1962. Superficially, the unspotted individuals are remarkably similar to *Tachys par* Darlington, but of course the frontal sulci are very different.

Tachys acuticollis Putzeys

Darlington 1962, Part I, p. 480.

Additional material. New material includes **N-E. N. G.**: 6, Okapa, Aug. 28, 1964 (Hornabrook). **West N. G.**: 7, Sibil Valley, Star Mts., 1245 m, Oct. 18–Nov. 8, 1961 (L. W. Quate, Bishop Mus.).

Notes. The series listed above consist of uniformly 2-spotted individuals, with posthumeral elytral spots but without subapical spots. The interrelation of 4-spotted *acuticollis*, the present 2-spotted form, and unspotted *coracinus* Putzeys requires further study based on series from additional localities. The color differences *may* prove to be Mendelian.

Tachys wallacei Andrewes

Darlington 1962, Part I, p. 479.

Additional material. **N-E. N. G.**: 1, Adelbert Mts.: Wanuma, 800–1000 m, Oct. 25, 1958 (Gressitt); 1, Finisterre Rge., Saidor: Gabumi Village, July 1–21, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Nabire, S of Geelvink Bay, 1–20 m, July 2–9, 1962 (Gressitt).

Notes. This rare, arboreal *Tachys* is evidently widely distributed in New Guinea, from sea level into the lower mountains.

Tachys yunax Darlington

Darlington 1939, Mem. Soc. Cubana Hist. Nat., 13: 87.

——— 1962, Part I, p. 482.

——— 1970, Insects of Micronesia. Coleop.: Carabidae, p. 19.

Louwerens 1967, Ent. Meddelelser, 35: 197 (referred to under *T. singularis* Andrewes).

Notes. T. yunax is now known from **New Guinea** and the **Aru Is.** (Darlington, 1962) and **Micronesia** (Darlington, MS) as well as from the Dominican Republic in the **West Indies** (Darlington, 1939). Louwerens (1967) suggests that *T. singularis* Andrewes (1925, Ann. Mus. Genoa, 51: 388, 393) of Celebes may be the same, in which case *yunax* will become a junior synonym of *singularis.* In any case this very widely distributed insect, which may be native in the Malay Archipelago, is probably carried by man, perhaps in wood or wood products of some sort.

Tribe TRECHINI

It is worth re-emphasizing that no *Trechus* and in fact no flightless mesophile Trechini of any sort have been found in New Guinea at any altitude.

Genus *PERILEPTODES* Jeannel

Darlington 1962, Part 1, p. 489.

Additional material of this genus will be reported on by Dr. Shun-Ichi Uéno. The genus has not been found at Wau.

Tribe PANAGAEINI

Darlington 1962, Part I, p. 492.
Jedlicka 1965, Annotationes Zool. et Bot. (Bratislava), No. 12: 1–15 (monograph of East Asiatic forms).

In 1962 I had seen only 7 specimens of this tribe from New Guinea, representing 3 genera and species. Eight additional specimens from the island are now before me, including 2 genera and 3 species not recorded before. Two of the species are striking novelties, based on unique specimens. The habitats of the members of this tribe in New Guinea are still wholly unknown.

Genus *TRICHISIA* Motschulsky
Trichisia papuana Csiki

Darlington 1962, Part I, p. 494.

Additional material. **Papua**: 1, Popondetta, 25 m, May 1966 (Shanahan-Lippert, Bishop Mus.), light trap; 1, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.).

Genus *PERONOMERUS* Schaum

Schaum 1853, Ann. Soc. Ent. France, (3) 1: 440.
Csiki 1928, Coleop. Cat., Carabidae, Harpalinae 1, p. 364 (see for additional references).
Jedlicka 1965, Annotationes Zool. et Bot. (Bratislava), No. 12: 2, 10.

Description. Small, unicolorous panagaeines; form characteristic (Fig. 19); surface punctate, pubescent; labrum with middle pair of setae not much farther forward than lateral setae; paraglossae not prolonged beyond apex of ligula; 4th hind-tarsal segments emarginate, with lobes not more than ½ total length of segment.

Type species. P. fumatus Schaum, of SE Asia, etc.

Generic distribution. **SE Asia** including **Japan** to the **Philippines** and **New Guinea** (not Australia).

Notes. Among genera of Panagaeini previously recorded from New Guinea (keyed out by me, 1962, Part I, p. 493) this is most like *Trichisia,* with which it shares short paraglossae (and uniform coloration), but *Peronomerus* differs from *Trichisia* in having the labrum with middle pair of setae not advanced and the prothorax more wedge-shaped.

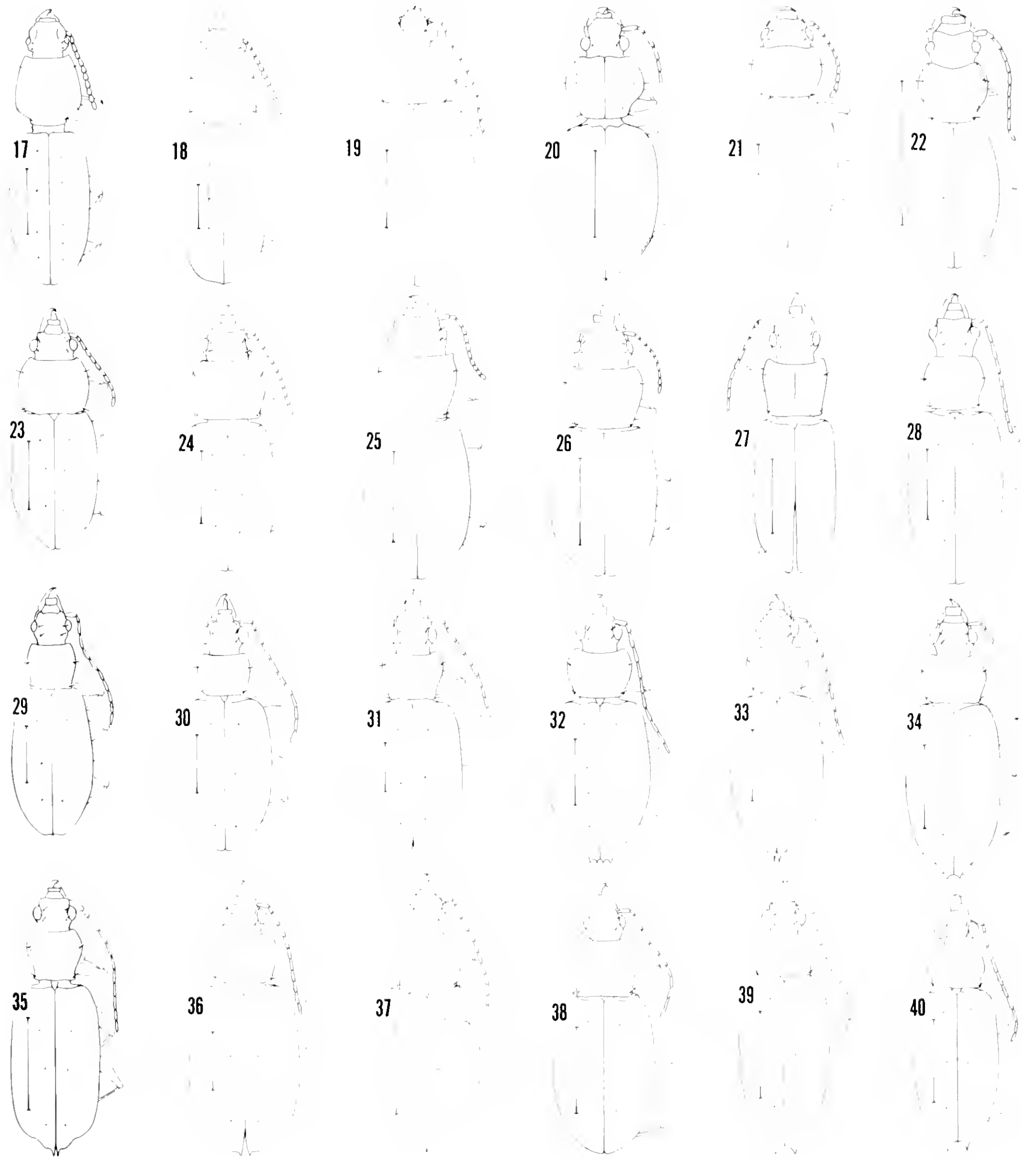
Although not recorded before, this genus does occur in New Guinea, where 1 Oriental and 1 endemic species are now known.

Key to Species of *Peronomerus* of New Guinea

1. Black; elytra coarsely punctate with striae well impressed; length *c.* 8–9 mm .... *xanthopus*
– Bluish green; elytra finely punctate with striae fine, superficial; length 10.8 mm .... *hornabrooki*

Peronomerus xanthopus Andrewes

Andrewes 1936, Treubia, 15: 217.



Figures **17–40** (see text, section [15]): **17**, *Clivina kubor* n. sp., holotype; **18**, *C. alternans* n. sp., holo.; **19**, *Peronomerus hornabrooki* n. sp., ♂ holo.; **20**, *Craspedophorus gressittorum* n. sp., ♂ holo.; **21**, *Mecyclothorax sedlaceki* n. sp., ♀ holo.; **22**, *Lesticus medius* n. sp., ♂ holo.; **23**, *Prosopogmus hornabrooki* n. sp., ♂ holo.; **24**, *P. sedlacekorum* n. sp., ♂ paratype; **25**, *Analoma rosenburgi* n. sp., ♀ holo.; **26**, *A. hornabrooki* n. sp., ♀ holo.; **27**, *Homalonesiota karawari* Maindron, ♀ holo.; **28**, *Notagonum curiosum* n. sp., ♂ holo.; **29**, *N. ambulator* n. sp., ♀ holo.; **30**, *N. astrum* n. sp., ♂ holo.; **31**, *N. exactum* n. sp., ♂ holo.; **32**, *N. quadruum* n. sp., ♂ para.; **33**, *N. sectum* n. sp., ♀ holo.; **34**, *Colpodes guega* n. sp., ♀ holo.; **35**, *C. helluo* Darl., ♀, Koibuga; **36**, *Iridagonum fessum* n. sp., ♀ para.; **37**, *I. vigil* n. sp., ♂ holo.; **38**, *I. septimum* n. sp., ♂ holo.; **39**, *Altagonum cheesmani* Darl., ♂, Wau; **40**, *A. sororium* n. sp., ♀ para., Tsenga.

Description. Form as usual in genus (cf. Fig. 19); black, appendages brownish testaceous, antennae browner except at base; extensively coarsely punctate above and below, moderately shining between punctures; elytral striae well impressed; length *c.* 8–9 mm.

Type. From **Java**, in British Mus. (seen).

Occurrence in New Guinea. **Papua**: 1, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.); 1, Popondetta, Northern District, Jan. 29, 1965 (Hornabrook).

Notes. Outside New Guinea, *xanthopus* is known from **Java** and the **Philippines**, and closely related forms occur north to South Asia and Japan.

Peronomerus hornabrooki n. sp.

Description. Form as in Figure 19; dark bluish green, legs red, antennae dark brown with 1st segments red; most of upper surface punctate and pubescent, shining between punctures. *Head* 0.58 width prothorax; impressed across base, irregularly channeled each side, punctate only at base especially laterally, smooth at middle; antennae with 3rd segments more than 2× long as 2nd; mentum with broad truncate tooth; ligula blunt, 1-setose each side; paraglossae not clearly visible. *Prothorax*: width/length 1.34; base/apex *c.* 2.29; sides abruptly sinuate before minute right posterior angles; setae at base and behind middle on each side; lateral marginal lines fine anteriorly, obsolete posteriorly; disc slightly depressed at sides posteriorly, with irregular middle line and deeper basal impressions; entire surface of disc closely coarsely punctate. *Elytra*: width elytra/prothorax 1.48; surface entirely closely finely punctate with rows of slightly coarser punctures indicating superficial striae. *Inner wings* fully developed. *Lower surface* punctate. *Legs*: 4th hind-tarsal segments shallowly emarginate. *Secondary sexual characters*: ♂ front tarsi not obviously modified; ♀ unknown. *Measurements*: length 10.8; width 4.9 mm.

Type. Holotype ♂ (MCZ, Type No. 31811) from Main River, Sepik, **N-E. N. G.**, Feb. 24, 1965 (Hornabrook).

Notes. The relatively fine punctation of the elytra (contrasting with the coarse punctation of the pronotum) distinguishes this from all previously known species of the genus.

Genus *MICROCOSMODES* Strand

Strand 1936, Folia Zool. et Hydrobiologica (Riga), 1936: 169.

Jedlicka 1965, Annotationes Zool. et Bot. (Bratislava), No. 12: 2, 6.

Microcosmus Chaudoir 1878, Ann. Soc. Ent. Belgique, 21: 85, 139 (not *Microcosmus* Fee 1830 nor Heller 1877).

Microschemus Andrewes 1940, Ann. Mag. Nat. Hist. (11), 5: 536.

Darlington 1962, Part I, p. 495.

Notes. I am indebted to Dr. Shun-Ichi Uéno for calling my attention to the preceding generic synonymy.

Microcosmodes quadrimaculatus (Csiki)

Darlington 1962, Part 1, p. 496 (*Microschemus*).

Additional material. **Papua**: 2, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.).

Notes. One of these specimens is not spotted (except that the prothoracic margins are pale posteriorly, as usual); the other, 4-spotted, each elytron with a very small anterior-lateral (chiefly on interval 8) and a subapical testaceous mark.

Genus *CRASPEDOPHORUS* auct.

Darlington 1962, Part I, pp. 492–493 (in text and key).

Notes. This genus, previously known from two separate areas (**SE Asia**, etc., and **Australia**) has not previously been recorded from **New Guinea**, but the following new species establishes its presence there.

Craspedophorus gressittorum n. sp.

Description. Form as figured (Fig. 20), moderately convex; black, appendages pic-

eous in part slightly reddish; elytra each with 2 yellow spots as figured; moderately shining, disc of pronotum and elytra finely lightly *c.* isodiametrically microreticulate, head and marginal and lateral channels and base of prothorax irregularly punctate. *Head* 0.60 width prothorax; antennae long (but outer 5 or 6 segments missing); mandibles short, with points overlapping; labrum emarginate, 4-setose, with 2 inner setae behind level of outer setae; clypeus truncate, 1-setose each side well behind anterior margin; front irregularly impressed each side; neck transversely impressed; mentum with truncate tooth; ligula and paraglossae fused, forming a single structure truncate (slightly arcuate) anteriorly with 1 seta each side. *Prothorax*: width/length 1.34; base/apex 1.15; margins wide; posterior angles obtuse but well-defined, each with seta at angle (no setae anteriorly); disc convex, middle line deep, transverse impressions obsolete. *Elytra*: width elytra/prothorax 1.32; humeri roundly prominent with margins elevated; striae moderately impressed on disc but very light (indicated by rows of punctures) externally; intervals *c.* equal. *Inner wings* presumably atrophied (not examined). *Lower surface*: metepisterna short, scarcely longer than wide; much of lower surface irregularly rather sparsely punctate, and abdomen also sparsely pubescent at middle (sterna also sparsely pubescent at middle); apical ventral segment with 2 seta-bearing punctures each side before apex. *Legs* slender; 4th hind-tarsal segments emarginate but not long-lobed. *Secondary sexual characters*: ♂ front tarsi slightly dilated, densely clothed below with slender squamules; ♂ apical ventral segment with 2 punctures close together on each side before apex; ♀ unknown. *Measurements*: length *c.* 12 mm; width 4.9 mm.

Type. Holotype ♂ (Bishop Mus.) Tapini (Goilala), **Papua**, 1100 m, May 18, 1961 (J. L. & M. Gressitt).

Notes. This new species has the elytra much more lightly striate than *C. australis* Dejean or any other member of the genus previously known to me.

Tribe PTEROSTICHINI
Genus *MORION* Latreille
Morion longipenne Putzeys

Darlington 1962, Part I, p. 503.

Additional material. Ninety-four, from many widely scattered localities; included are many from Wau, etc., altitudes up to 1700–1800 m, dates in every month *except* April (Sedlaceks and others).

Notes. The numerous specimens assigned to this species vary considerably, as noted by me in 1962. This and related species in the Malay Archipelago require third-stage taxonomic study.

Genus *MECYCLOTHORAX* Sharp

Darlington 1962, Part I, p. 505.

Mecyclothorax sedlaceki n. sp.

Description. Form as figured (Fig. 21); rather strongly convex; black, appendages slightly rufescent; reticulate microsculpture light or indistinct on front and pronotum, more distinct and irregular but *c.* isodiametric on elytra. *Head* 0.77 width prothorax; eyes moderate, genae shorter than eyes, oblique, very slightly arcuate; antennae rather short, middle segments not more than 1½ × as long as wide; front convex, clypeal suture well impressed, frontal impressions slightly irregular but linear and subparallel; 2 setae over each eye; mentum with strong rounded tooth. *Prothorax* slightly transverse-rounded; width/length 1.36; base/apex 0.98; base/head 0.94; sides *c.* rounded to base except very briefly strongly sinuate just before right subdentiform posterior angles; margins narrow, each with seta at basal angle and ⅓ from apex; disc with fine middle line and transverse impression and with basal area slightly depressed and conspicuously punctate. *Elytra* 1.46 width prothorax, quadrate-oval, slightly narrowed anteriorly to broadly rounded humeri; subapical sinuations slight; anterior margin entire, connected to scutellar striae; striae light, slightly impressed near suture, reduced externally to rows of punctures; 7th

striae scarcely indicated; 3rd intervals each with 2 or 3 seta-bearing punctures, 5th intervals apparently without such punctures. *Inner wings* apparently atrophied. *Lower surface* virtually impunctate except a few punctures at sides of mesosterna. *Legs* without noteworthy special characters. *Secondary sexual characters*: ♀ last ventral segment with 2 pairs of setae each side near apex and an additional pair of smaller setae close together at middle farther from apex; ♂ unknown. *Measurements*: length 4.3 mm; width 1.8 mm.

Type. Holotype ♀ (Bishop Mus.) from Mt. Wilhelm, Bismarck Rge., **N-E. N. G.**, 4250 m, June 3, 1963 (J. Sedlacek); the type is unique.

Notes. The only species of the genus previously known from New Guinea is *M. toxopei* Darlington (1962, Part I, p. 506), known from a single specimen from 4200 m on Wilhelminatop, Snow Mts., West N. G. The present new species evidently represents the same stock but differs from *toxopei* slightly in details of form (more distinct posterior prothoracic angles, etc.) and especially in having the base of the pronotum extensively and conspicuously punctate and the elytral striae punctate, and in lacking seta-bearing punctures on the 5th elytral intervals. See section [80] of the present paper for further discussion of the distribution and probable history of this genus.

Genus *BRACHIDIUS* Chaudoir

Brachidius crassicornis Chaudoir

Darlington 1962, Part I, p. 508.

Additional material. Twenty-one, from various localities, including 1, Wau, 1200 m, Jan. 4–15, 1965 (M. Sedlacek).

Notes. Individuals of this species vary considerably in size. Those from montane localities tend to be larger.

Genus *CAELOSTOMUS* Macleay

Darlington 1962, Part I, p. 508.

Notes. Additional material (65 specimens) includes the following from vicinity of Wau.

C. novae-guineae Straneo, 1000–1300 m (1 individual)
C. albertisi Straneo, 1200 m (1)
C. subsinuatus (Chaudoir), altitudes from 1000 to 1700 m (7)
C. picipes Macleay, 1200, 1300 m (9)

Genus *COSMODISCUS* Sloane

Cosmodiscus rubripictus Sloane

Darlington 1962, Part I, p. 514.

Additional material. **Papua**: 1, Tapini (Goilala, Owen Stanley Rge.), May 17–19, 1961 (Gressitt), in light trap; 1, same locality, 975 m, Nov. 16–25, 1957 (W. W. Brandt, Bishop Mus.). **N-E. N. G.**: 8, Wau, 1200 m, dates in Jan., Feb., Apr., July, Sept. 1963, 1964 (Sedlaceks), some in m. v. light trap; 1, Okapa, June 13, 1965 (Hornabrook); 1, Torricelli Mts., Mobitei, 750 m, Apr. 16–22, 1959 (W. W. Brandt, Bishop Mus.); 1, Wapenamanda, West Highlands, Mar. 21, 1960 (J. Barrett, Dept. Agr. Port Moresby) at m. v. light.

Notes. All the specimens listed above are rather small (like the pair previously recorded from Dobodura) and all have at least vestiges of a red elytral pattern. Besides these specimens I have seen 2 others as follows. **N-E. N. G.**: 1, Damanti, Finisterre Rge., 3550 ft. (*c.* 1080 m), Oct. 2–11, 1964 (Bacchus, British Mus.), "Station No. 46"; 1, Budemu, Finisterre Rge., *c.* 4000 ft. (1220 m), Oct. 15–24, 1964 (Bacchus, British Mus.), "Station No. 51." These 2 specimens are identified doubtfully. The one from Damanti is more parallel-sided than most *rubripictus* and lacks red marks, and the surface seems to be modified perhaps by a chemical preservative. The one from Budemu is much larger (*c.* 8.3 mm), unmarked except for slightly reddish suture and slight translucent lateral prothoracic margins, and very deeply striate. However, these specimens show no decisive differences from *rubripictus*, and they may represent extremes of a population that varies in size, markings, and some other details.

Cosmodiscus brunneus Darlington

Darlington 1962, Part I, p. 515.

Additional material. **N-E. N. G.**: 4, Wau, 1200 m, Sept. 17, Nov. 21, 1961 (Sedlaceks), some at m. v. light trap; 1, Lae, Singuawa R., 30 m, Apr. 15, 1966 (Lippert, Bishop Mus.); 1, Torricelli Mts., Mobitei, 750 m, Feb. 28–Mar. 4, 1959 (W. W. Brandt, Bishop Mus.).

Genus *LESTICUS* Dejean

Darlington 1962, Part I, p. 521.

Notes. Thirty additional specimens from New Guinea have been seen. They are referred (in some cases doubtfully) to *chloronotus* Chaudoir (subspecies?), *gracilis* Darlington, *politus* Chaudoir, and a new species from the Wissel Lakes described below. Third-stage taxonomic study, based on much more material, is needed to determine specific variation and specific limits in this genus. No species of the genus has yet been found at or near Wau.

Lesticus medius n. sp.

Description. With characters of genus; form as figured (Fig. 22), with elytra more narrowed in front than behind; moderately depressed; black, elytra slightly aeneous, appendages dark; moderately shining, reticulate microsculpture indistinct on head and pronotum, light and very fine on elytra. *Head* 0.77 and 0.79 width prothorax; eyes moderate; antennae with middle segments 3× long as wide; mandibles strongly curved and acutely produced as usual; front weakly irregularly convex, deeply impressed each side anteriorly; neck constriction slight. *Prothorax* cordate; width/length 1.37 and 1.45; base/apex 0.95 and 0.87; lateral margins rather narrow, each with usual 2 setae; disc weakly convex, with fine middle line and weak (subobsolete) transverse impressions; basal foveae shallow and poorly defined, impunctate. *Elytra*: width elytra/prothorax 1.30 and 1.31; humeri narrowed, obtuse; subapical marginal interruption present; striae virtually absent or indicated as faint fine lines; each elytron with 2 minute punctures on (position of) 3rd interval, on outer edge less than ¼ from base and inner edge near middle (posterior dorsal punctures absent). *Inner wings* vestigial, reduced to thin strips *c.* ⅓ length elytra. *Lower surface* impunctate except for group of punctures each side mesosternum; metepisterna shortened, slightly longer than wide. *Secondary sexual characters*: ♂ front tarsi slightly dilated, 3 segments squamulose below; ♂ with 1, ♀ with 2 setae each side last ventral segment. *Measurements*: length 19.0–20.5 mm; width 6.7–7.5 mm.

Types. Holotype ♂ (MCZ, Type No. 31813) from Kamu Valley, Wissel Lakes, **West N. G.**, June–Aug. 1959 (L. J. Pospisil); I am indebted to Professor C. T. Remington for this specimen. Also 10 paratypes (some in MCZ) all from Lake Paniai, Wissel Lakes, 1750 m, Sept. 23, 28, 30, Oct. 1, 1939 (H. Boschma, Leiden Mus.).

Measured specimens. The ♂ holotype and one ♀ paratype.

Notes. In my key to New Guinean *Lesticus* (1962, Part I, pp. 523–524), this species would run to couplet 5, but would fit neither half of the couplet, being less broad and less depressed than *depressus* but broader and less convex than *toxopei* and *ambulator*. Actually, the present new species is intermediate between the normally formed, fully winged members of the genus and the more strongly modified flightless forms just named. In other words, the present new species represents an intermediate stage in wing atrophy leading toward the more highly divergent montane species.

Genus *PROSOPOGMUS* Chaudoir

Darlington 1962, Part I, p. 536.

KEY TO SPECIES OF *PROSOPOGMUS* OF NEW GUINEA

1. Fully winged; pronotum punctate baso-laterally .... *garivagliae*
– Wings atrophied; pronotum not or not much punctate baso-laterally 2
2. Eyes larger (cf. Figs. 23 and 24); prothorax relatively wider and with wider base (cf. proportions in *Descriptions*) .... *hornabrooki*

– Eyes smaller; prothorax relatively narrower and with narrower base .... *sedlacekorum*

Prosopogmus garivagliae Straneo

Darlington 1962, Part I, p. 537.

Additional material. Thirty-one, from widely scattered localities; altitudes given from 50 to 1950 and 1665–2530 m; included are 6 from Wau, 1050, 1200 m, dates in Jan., Sept., Oct., Nov., Dec., 1961–1963 (Sedlaceks and others), some in light traps.

Notes. This species varies in depth of striae and in other ways and requires third-stage study.

Prosopogmus hornabrooki n. sp.

Description. With characters of genus; form as figured (Fig. 23); black, appendages reddish black; shining, reticulate microsculpture indistinct on head, very light and slightly more distinct and transverse on elytra. *Head* 0.68 width prothorax; eyes slightly larger and meeting neck more abruptly than in other New Guinean members of genus; front convex except for transverse clypeal suture and curved anterior frontal impressions. *Prothorax* moderately transverse; width/length 1.37; base/apex 1.33; lateral margins rather narrow; disc weakly convex, distinctly flattened each side near basal angle, with middle line fine and abbreviated both ends, transverse impressions obsolete, and basal impressions sublinear; surface of disc impunctate except for a few punctures basally especially near lineal basal impressions (not near angles). *Elytra* subquadrate, not noticeably narrowed basally; width elytra/prothorax 1.18; striae entire, deeply impressed, not punctate; intervals convex, 3rd 3-punctate with anterior puncture on outer and others on inner edge of interval. *Inner wings* reduced to thin strips *c.* ⅗ length elytra. *Lower surface*: last 3 ventral segments transversely impressed near base. *Secondary sexual characters*: ♂ front tarsi moderately dilated, 3 segments squamulose; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements*: length 9.5; width 3.5 mm.

Type. Holotype ♂ (MCZ, Type No. 31814), from Okapa (SW of Kinantu, East Highlands), **N-E. N. G.**, (altitude probably between 1650 and 1800 m), June 12, 1964 (Hornabrook); the type is unique.

Notes. This new species is close to *garivagliae* Straneo (preceding) but has a more transverse prothorax with pronotum less punctate basally, relatively larger eyes, and reduced inner wings. *P. garivagliae* occurred at Okapa too, which suggests that *hornabrooki* is a real species, not a geographic form. The fact that the eyes are relatively larger in *hornabrooki* in spite of the fact that the wings are reduced also suggests specific distinctness.

Prosopogmus sedlacekorum n. sp.

Description. With characters of genus; form as in Figure 24, rather slender; black, appendages reddish black; shining, reticulate microsculpture faint or light and isodiametric on head, more distinct and more transverse on pronotum and elytra. *Head* 0.71 and 0.73 width prothorax; front evenly convex except for deep clypeal suture and curved anterior impressions each side, with surface finely rather sparsely punctulate. *Prothorax* subquadrate; width/length 1.29 and 1.33; base/apex 1.23 and 1.18; lateral margins relatively narrow; disc normally convex, less impressed than usual baso-laterally, with fine middle line, transverse impressions obsolete; surface impunctate, except vaguely punctate baso-laterally. *Elytra* slightly narrowed anteriorly; width elytra/prothorax 1.24 and 1.24; striae entire, moderately convex, 3rd 3-punctate with 1st puncture on outer and others on inner edge of interval. *Inner wings* vestigial, reduced to narrow strips *c.* ⅓ length of elytra. *Lower surface*: last 3 ventral segments conspicuously transversely impressed near base. *Secondary sexual characters*: ♂ front tarsi moderately dilated, 3 segments squamulose below; ♂ with 1, ♀ 2 setae each side last ventral segment. *Measurements*: length 9.3–10.4 mm; width 3.5–3.8 mm.

Types: Holotype ♂ (Bishop Mus.) and

4 paratypes (2 in MCZ, Type No. 31815) all from Mt. Giluwe, **Papua**, with additional details as follows: holotype, 2500–2750 m, May 30, 1963; paratypes, 2500, 2550, 2800–3280 m, dates in May 1963 (all specimens collected by J. and/or M. Sedlacek).

Measured specimens: the ♂ holotype and ♀ paratype from 2550 m.

Notes. This distinct, localized, flightless species is distinguished from other New Guinean members of the genus in the preceding key.

Genus *ANALOMA* new name

Paraloma Darlington 1962, Part I, pp. 500, 538 (not *Paraloma* Cope 1863, Proc. Acad. Nat. Sci. Philadelphia for 1962: 181).

Diagnosis and description. As for *Paraloma* Darlington 1962.

Type species. Paraloma fortis Darlington 1962, p. 539.

Generic distribution (revised). High mountains of **New Guinea**.

Notes. The name *Analoma*, now proposed, is a new name for *Paraloma* Darlington, which is preoccupied. I am indebted to Mr. W. J. Brown for calling my attention to Cope's earlier use of *Paraloma*.

The 2 new species described below extend the range of the genus, previously known only from the Snow Mts., West N. G., to mountains in the eastern half of the island.

KEY (REVISED) TO THE SPECIES OF *ANALOMA*

1. Elytra with basal margin 2
- Elytra without basal margin .... *gracilis*
2. Sides of prothorax not sinuate .... *hornabrooki*
- Sides of prothorax sinuate posteriorly 3
3. Sides of prothorax sinuate farther before base (Darlington 1962, fig. 56) .... *fortis*
- Sides of prothorax sinuate very near base (present Fig. 25) .... *rosenburgi*

Analoma rosenburgi n. sp.

Description. With characters of genus; form as in Figure 25 (but possibly dimorphic); black (slightly reddish), appendages reddish brown; shining, reticulate microsculpture of front and pronotum indistinct, of elytra very fine, lightly impressed, slightly transverse. *Head* 0.79 width prothorax; eyes small (but longer than genae), scarcely prominent; mentum tooth broad, short, emarginate; other mouthparts as described for genus (1962). *Prothorax* very broad anteriorly (but perhaps dimorphic); width/length 1.28; base/apex 0.84; base/head 0.96; lateral margins narrow, slightly broader at anterior angles, still broader (but not wide) at base, each with seta-bearing puncture *c.* ⅓ from apex just inside margin and on face (not edge) of margin at base; basal sinuations of margin strong, very near *c.* right (slightly acute) basal angles; disc with usual impressions weak, baso-lateral impressions slight and poorly defined; base and apex not margined; apical angles prominent, bluntly acute. *Elytra* narrowed toward base; width elytra/prothorax 1.36; base margined, margin obtusely but distinctly angulate at humeri; humeri not dentate; subapical marginal interruptions present; subapical sinuations slight; apices conjointly rounded; striae slightly impressed, virtually entire, irregularly punctulate; no ocellate puncture at base; 3rd intervals impunctate (as usual in genus). *Lower surface* and *legs* as described for genus (1962). *Secondary sexual characters* of ♀ normal, of ♂ unknown. *Measurements*: length 12.6; width 4.8 mm.

Type. Holotype ♀ (MCZ, Type No. 31817) from Mt. Albert Edward, **Papua**, 13,200 ft. (*c.* 4025 m), July 1, 1963 (Guy Rosenburg), in alpine grassland; the type is unique.

Notes. This species probably represents the same stock as *Analoma fortis* (Darlington) (1962, Part I, p. 539) of the Snow Mts., West N. G., but differs as indicated in the preceding *Key*. *A. rosenburgi* may prove to be dimorphic in form, as *fortis* is.

I take pleasure in naming this interesting new, high-altitude species for the collector.

Analoma hornabrooki n. sp.

Description. With characters of genus; form as in Figure 26 (but perhaps di-

morphic); black, appendages dark brownish; shining (although surface partly obscured), reticulate microsculpture light, fine and irregular on head, indistinct on pronotum, rather strongly transverse on elytra. *Head* 0.76 width prothorax; eyes rather large (in genus), slightly prominent and longer than genae; mentum tooth very wide, short, emarginate; other mouthparts as described for genus (1962). *Prothorax* subcordate; width/length 1.30; base/apex 1.00; base/head 1.00; lateral margins very narrow anteriorly, wider posteriorly, running into shallow poorly defined baso-lateral impressions, with setae as described for preceding species (*rosenburgi*); base and apex not margined; disc with fine middle line, very weak transverse impressions, scarcely sculptured at base. *Elytra* narrowed toward base; width elytra/prothorax 1.34; base margined, margin *c.* right (slightly obtuse) at humeri; subapical marginal interruptions present; subapical sinuations moderate; apices conjointly rounded; striae slightly impressed, entire, irregularly punctulate at least in part; intervals scarcely convex, irregularly sparsely punctulate; ocellate puncture at base 1st stria, but 3rd interval impunctate. *Lower surface* and *legs* as described for genus (1962) except proepisterna in part finely punctate. *Secondary sexual characters* of ♀ normal; of ♂ unknown. *Measurements*: length 12.0; width 4.7 mm.

Type. Holotype ♀ (sex determined by dissection) (MCZ, Type No. 31816) from Okapa (Purosa), **N-E. N. G.**, (altitude probably between 1650 and 1800 m), Nov. 30, 1965 (Hornabrook); the type is unique.

Notes. Although this species differs considerably in form from *A. rosenburgi*, both species may prove to be dimorphic, as *fortis* is known to be on the Snow Mts., so that form may prove not to be specifically diagnostic. However, the present new species differs from the preceding one (*rosenburgi*) in other ways, including presence of an ocellate puncture at the base of the first striae (absent in *rosenburgi*) and much more transverse elytral microsculpture. I have no doubt that the single individuals on which these species are based represent distinct, local, high-altitude forms of a group of which other representatives will probably be found on other mountains widely scattered over New Guinea.

This species, like several others in the present paper, is dedicated to Dr. R. Hornabrook, in recognition of his discoveries of exciting Carabidae at high altitudes in New Guinea.

Genus *HOMALONESIOTA* Maindron

Darlington 1962, Part I, p. 516.

Description, *Notes*, etc. See under following species.

Homalonesiota karawari Maindron

Maindron 1908, Nova Guinea, 5: 296.
Andrewes 1946, Proc. R. Ent. Soc. London, ser. B, p. 85.
Darlington 1962, Part I, p. 517.

Description (*revised*). Form and selected details as in Figure 27; head and pronotum without distinct microsculpture, elytra with meshes distinct, irregular, transverse but not close-packed (not iridescent). *Head* (as measured in type) 0.79 width prothorax; clypeus 1-setose each side (and apparently impressed or punctate at outer corners of base); labrum 6-setose; mentum with simple triangular tooth; ligula not clearly visible; paraglossae longer, rather narrow, membranous; mandibles without seta in scrobe. *Prothorax* subquadrate; width/length 1.26; base/apex 0.98; lateral margins narrow, each with seta just inside margin *c.* 1/3 from apex and seta on raised margin just before base; base and apex not margined at middle; disc with median impressed line fine, abbreviated both ends, transverse impressions weak, baso-lateral impressions irregularly linear, they and surface near them punctate. *Elytra* parallel; width elytra/prothorax 1.27; base margined, margin obtusely angulate at humeri; basal margin running into 1st striae; no scutellar striae; ocellate puncture at base 2nd stria; *subapical marginal interruptions absent*;

striae impressed, impunctate; intervals slightly convex, 7th and 8th slightly narrowed and more convex toward apex but not otherwise modified, punctures (ocellate) of 9th intervals as indicated (Fig. 27); 10th intervals absent; subapical puncture between striae 7 and 8; single dorsal puncture on 3rd interval of each elytron as indicated (Fig. 27). *Inner wings* full (visible). *Lower surface*: sterna and 1st ventral segment partly, irregularly punctate; last ventral entire, 2-setose each side (♀). *Legs* moderately slender; hind trochanters nearly ½ long as femora, rather narrowly oval, narrowly rounded at apex; hind tibiae grooved each side externally but not grooved at middle; hind tarsi with basal segments subcarinate at middle and each side above, rather broadly slightly depressed (rather than sulcate) between median and lateral carinae; 4th hind-tarsal segments weakly emarginate; 5th segments with 1 or 2 weak accessory setae each side (additional setae possibly broken off). *Length* c. 10.2 mm.

Type. Holotype ♀ (Paris Mus.) labeled "Tawarw./Juni 1903," "nieuw. Guinea./ Expeditie 1903," "Homalonesiota karawari m. [on small red square]" "Collection Babault." An additional label repeats the name, gives the original reference, and notes that the specimen was submitted to Andrewes 27/7/1922. This specimen (the type) is now in the Paris "Generale" collection in a box with New Zealand *Holcaspis*, etc., the box being apparently numbered 19.

Occurrence in New Guinea. Known only from the type.

Notes. Andrewes was seriously in error in comparing this insect to *Morion*. The resemblance is superficial. In fact, many characters indicate an actual relationship with *Loxandrus*. The general form is rather like that of a parallel-sided *Loxandrus*, and the linear baso-lateral prothoracic impressions and single dorsal elytral punctures are consistent too. Also consistent is the absence of an interruption of the elytral margin toward the apex. This interruption is rarely absent in Pterostichini but does vary and is sometimes obliterated in *Nebrioferonia*, which is (I think) a *Loxandrus*-derivative. The form of the ♂ front tarsi of *Homalonesiota karawari* is of course unknown, since the type is a ♀. However, this beetle is so similar in other ways to the species that I have described as *Nebrioferonia straneoi* (below) that I feel sure the ♂ tarsi will be the same. I am therefore transferring *straneoi* to *Homalonesiota*. The 2 species, *karawari* and *straneoi*, differ mainly in form, the prothorax of *straneoi* being much more narrowed posteriorly and the elytra coaptively narrowed toward base. The two species agree in lacking or virtually lacking the marginal interruptions of the elytra as well as in many other characters. The type species of *Nebrioferonia*, *strigitarsis* Straneo, differs in some details that may permit retention of Straneo's genus. I shall let future revisers of the *Loxandrus* complex decide about this.

It seems likely that *H. karawari* and *H. straneoi*, like *Nebrioferonia strigitarsis*, live among cobblestones and under other cover by running water, although there is no actual record of this. It is surprising that no additional specimens of *karawari* have been found, since it is a winged species occurring at low altitudes. It may prove to be a primarily lowland form which is replaced at higher altitudes by *straneoi*.

Homalonesiota straneoi (Darlington)

Darlington 1962, Part I, p. 559 (*Nebrioferonia*).

Additional material. **N-E. N. G.**: 15, Wau, Morobe Dist., 1200 (most), 1250 (1) m, dates in Jan., Mar., Apr., May, Sept., Oct., Nov., Dec., 1961–1966 (Sedlaceks, and 1 Gressitt & Wilkes), some labeled as taken in light trap or m. v. light trap; 1, 6 km W of Wau, Nami Ck., 1700 m, June 10, 1962 (Sedlacek), in Malaise trap; 1, Mt. Kaindi, 2350 m, Dec. 12, 1964 (Sedlaceks); 1, W Highlands, nr. Minj, 1340 m, May 2, 1966 (Gressitt), light trap; 1, Eliptamin Vy., 1200–1350 m, July 16–31, 1959 (W. W. Brandt, Bishop Mus.); 1, Finisterre Rge., Moro, *c*. 5550 ft. (*c*. 1700 m), Oct. 30–Nov.

15, 1964 (Bacchus, British Mus.). **West N. G.**: 1, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Notes. The **N-E. N. G.** records fill the previous geographic gap in the species' distribution. It was known formerly only from the Snow Mts., **West N. G.**, and Kokoda, **Papua**.

Genus *NEBRIOFERONIA* Straneo

Darlington 1962, Part 1, p. 557.

Notes. See *Notes* under *Homalonesiota karawari* (above).

Nebrioferonia strigitarsis Straneo

Additional material. **N-E. N. G.**: 1, Wau, Mt. Missim, 1250 m, Oct. 5, 1961 (Sedlaceks); 2, Main R., Sepik, Feb. 1965 (Hornabrook). **West N. G.**: 2, Star Rge., Sibil, 1260 m, June 27, 29, 1959 (Neth. N. G. Exp., Leiden Mus.); 1, Sentani, 90+ m, June 22, 1959 (Gressitt & Maa), m. v. light trap.

Notes. This species may vary geographically, but more material is needed to treat it properly. It lives among cobblestones, etc., beside fairly large streams.

Tribe AGONINI

Darlington 1952, Part II, p. 113.

——— 1956, Australian carabid beetles III. Notes on the Agonini. Psyche, 63: 1–10.

——— 1963, Australian carabid beetles XIII. Further notes on Agonini, . . . Breviora (Museum of Comparative Zoology), No. 183: 1–10.

In 1952, in Part II of my work on carabid beetles of New Guinea, 18 genera, 107 species, and 14 additional subspecies of Agonini were recognized from the island. Since then, "*Colpodes*" *violaceus* Chaudoir has been made the type of a new genus (*Violagonum*) by me in 1956, and 2 additional genera are recorded now. One, *Dicranoncus*, is expected. The other, *Agonum*, is unexpected. This genus is dominant in the northern hemisphere; the single stock (subgenus *Sericoda*) that has reached New Guinea has evidently done so by "mountain-hopping." One common south-temperate Australian species, *Notagonum submetallicum* (White), has been found to occur in the Wissel Lakes region in the mountains of central New Guinea. And 50 new, chiefly mountain-living species, some of them strikingly characterized, have been discovered and are described below; their discovery has necessitated complete revisions of several of the mountain-living genera. These additions bring the number of Agonini known from New Guinea to 21 genera, 160 species, and 14 additional subspecies. This total will surely be very much increased by further collecting on the higher mountains of the island.

The origins and radiation of Agonini on New Guinea are discussed in Part II and summarized in the present part [92].

Agonini are dominant throughout the tropics of the world, but are relatively less numerous in most temperate areas and notably few in Australia. The change from an overwhelmingly agonine fauna in New Guinea to an overwhelmingly pterostichine fauna in Australia has been discussed by me in 1956 and is rediscussed in the present paper [64].

The following characters are considered normal for Agonini and will usually not be repeated in the individual descriptions, unless the normal characters are modified. (A more detailed discussion of structures and characters of New Guinean Agonini will be found in Part II, pages 94ff.) On the *upper surface*, the reticulate microsculpture is considered normal when the meshes are visible in good light at a magnification of 54×, and when they are isodiametric on head, moderately transverse on pronotum, and equally or more transverse on elytra. On the *head*, the eyes are normally prominent, with 2 setae over each eye; mandibles, of moderate length and moderately arcuate; the palpi, not or not much dilated; and the mentum, with a triangular tooth. The *prothorax* normally has lateral margins moderate, wider posteriorly, each with 2 setae, at or near basal angle and slightly before middle; disc with rather fine impressed middle line usually abbreviated

at both ends, less well-defined anterior and posterior transverse impressions, and moderate, usually impunctate baso-lateral impressions. The *elytra* normally have margins with moderate subapical sinuations; 8 entire, moderately impressed striae (in addition to the scutellar striae); and intervals usually not much modified toward apex, the third with 3 seta-bearing punctures more or less evenly spaced along the length of the interval, the anterior puncture being on the outer and the other punctures on the inner edge of the interval. The *lower surface* is normally impunctate or nearly so, and not pubescent except for fixed setae. And normal *secondary sexual characters* are ♂ with anterior tarsi slightly dilated, the first 3 segments 2-seriately squamulose; and ♂ with 1, ♀ 2 setae each side last ventral segment.

THE KEY TO GENERA OF AGONINI OF NEW GUINEA (Part II, pp. 114–116) may be brought up to date by insertion of the following couplets:

9a. Fifth hind-tarsal segments with accessory setae; ♂ parameres tipped with setae .... *Agonum* (*Sericoda*)
– Fifth hind-tarsal segments without accessory setae; ♂ parameres without setae .... *Notagonum*
10a. Head relatively short, with short mandibles; (broad, purple, each elytron with an apical spine *c.* opposite 2nd interval, length *c.* 10 mm) .... *Violagonum*
– Head and mandibles relatively longer; (form and color various, elytra differently spined or not spined, size usually larger) .... *Colpodes*

Note also the following exceptions to characters used in the original *Key*: *Notagonum* now includes 1 species with reduced wings (*ambulator*, described below), and *Altagonum* now includes 2 species which have lost the anterior supraocular setae (*bigenum* and *conicolle*, described below).

Genus *ARHYTINUS* Bates

Arhytinus medius Darlington

Darlington 1952, Part II, p. 117.

Additional material. Six, from localities scattered in all three political divisions of New Guinea; most at low altitudes, but 1, Tapini (**Papua**), at probably *c.* 1200 m.

Arhytinus granum Darlington

Darlington 1952, Part II, p. 119.

Additional material. **N-E. N. G.**: 1, Okapa, probably between 1650 and 1800 m, June 13, 1965 (Hornabrook).

Notes. This very small agonine has been known before only from the 2 types from Dobodura.

Genus *TARSAGONUM* Darlington

Darlington 1952, Part II, p. 120.
Louwerens 1966, Ent. Tidskrift, 87: 36.

Generic distribution (revised). Known only from **New Guinea** and **Borneo**.

Notes. This very distinct genus was originally based on the single New Guinean species; the Bornean species has been described by Louwerens (1966).

Tarsagonum latipes Darlington

Darlington 1952, Part II, p. 120.

Additional material. **Papua**: 1, Mt. Dayman, Maneau Rge., 700 m, "N. Slope No. 6," July 13–20, 1953 (Geoffrey M. Tate, AMNH). **N-E. N. G.**: 1, Torricelli Mts., Mobitei, 750 m, Feb. 28–Mar. 4, 1959 (W. W. Brandt, Bishop Mus.).

Notes. Previously known only from the type series from Dobodura.

Genus *EUPLENES* Schmidt-Goebel

Euplenes laetus Darlington

Darlington 1952, Part II, p. 122.

Additional material. **N-E. N. G.**: 1, Wau, Morobe Dist., 1200 m, Dec. 18, 1961 (Sedlaceks); 1, Sepalakambang, Salawaket Rge., 1920 m, Sept. 15, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Wareo, Finschhafen (Finch Haven) (L. Wagner, South Australian Mus.). **West N. G.**: 1, Star Rge., 1300

m, Bivak 39, July 26, 1959, and 1, Star Rge., 1500 m, "mond Ok tenma," May 18, 1959 (both Leiden Mus., Neth. N. G. Exp.).

Notes. This is evidently primarily a mountain-living species.

Euplenes apicalis Darlington

Darlington 1952, Part II, p. 123.

Additional material: 104, from many localities in **Papua** (including 44 additional specimens from Dobodura, the type locality) at low altitudes and in mountains up to Wau (many specimens, but none certainly above 1250 m); Kassem Pass, **N-E. N. G.**, 1460 m; and Mt. Giluwe, **Papua**, 2550 m.

Genus *DICRANONCUS* Chaudoir

Dicranoncus queenslandicus (Sloane)

Darlington 1952, Part II, p. 124.

Occurrence in New Guinea. **N-E. N. G.**: 22, Wau, Morobe Dist., 1050, 1200 m, dates in Feb., Mar., May, July, Oct., Nov., Dec., 1961–1964 (Sedlaceks), some in m. v. light trap; 3, Western Highlands, Baiyer R., 1150 m, Oct. 18, 19, 1958 (Gressitt); 1, Finschhafen, Huon Pen., 10 m, Apr. 16, 1963 (Sedlaceks), m. v. light trap.

Notes. As I stated in 1952, this species, although previously unrecorded from New Guinea, is known from many localities from **India** and **Ceylon** to **NE Australia**. It probably inhabits grassland. The length of New Guinean specimens is 6.6–7.2 mm.

Genus *AGONUM* Bonelli

Subgenus *SERICODA* Kirby

Kirby 1837, Richardson's Fauna Boreali-Americana, 4: 14.

Tanaka 1960, Kontyu, 28: 90.

Lindroth 1966, Opuscula Ent., Supplementum 29: 565.

Diagnosis. Small, often flattened, parallel-sided, black Agonini with rather short antennae; with full complement of 2 pairs supraocular and 2 pairs lateral prothoracic setae and 3 punctures on 3rd elytral interval; 5th hind-tarsal segments with accessory setae; ♂ copulatory organs with both parameres tipped with setae.

Description. None required here.

Type species. *Agonum bembidioides* Kirby, of North America.

Subgeneric distribution. Previously known to be **circumpolar** in the northern hemisphere south to the **Himalayas**, **Japan**, and **Formosa** (only at high altitudes on latter, according to Uéno, personal communication); now found to be represented also (by *A. ceylanicum*, below) in tropical Asia and on islands east to the **Philippines** and **New Guinea**. Besides *A. ceylanicum*, a second species of *Sericoda* has been found in the Philippines: *Agonum* (*Sericoda*) *quadripunctatum* De Geer, a northern circumpolar species previously known to reach the Himalayas and Japan, occurs also on Luzon (specimens in British Museum with Böttcher's field Nos. 167 and 169, indicating "Haights-pl(ace)," at high altitudes in the mountains near Baguio, March 1912).

Notes. The occurrence of *Sericoda* in New Guinea is the first proven occurrence of any primarily north-temperate group of *Agonum* so far east and south in the Indo-Australian Archipelago.

According to Lindroth, the species of *Sericoda* "are excellent flyers and share a biological property, not yet understood: they are attracted by burning wood and sometimes appear in great number during and after forest fires, . . . when the ashes are still hot."

Agonum (*Sericoda*) *ceylanicum* (Motschulsky)

Motschulsky 1859, Etude Ent., 8: 36 (*Agonothorax*).

Andrewes 1930, Cat. Indian Carabidae, p. 24 (*Anchomenus*).

——— 1931, J. Federated Malay Mus., 16: 436 (*Anchomenus*).

——— 1933, Cat. Carabidae Sumatra, p. 328.

——— 1947, Arkiv f. Zoologi, 38, No. 20: 9.

Landin 1955, Arkiv f. Zoologi, ser. 2, 8: 403, 441.

philippinense Jedlicka 1935, Acta Soc. Ent. Czechoslovakia, 32: 79 (NEW SYNONYMY).

?*karasawai* Tanaka 1960, Kontyu, 28: 91, 94, figs. 2, 5 (NEW SYNONYMY).

Types. Of *ceylanicum*, from **Ceylon**, should be in Moscow University Museum; of *philippinense*, from the **Philippines**, in British Museum (the type has Böttcher's field No. 46, which, according to his not-very-legible notebook, indicates the locality Mt. Polis, apparently in Mindanao, Feb. 1918); of *karasawai*, from **Japan**, in Karasawa's collection. (Of these, only the type of *philippinense* has been seen.)

Description (for recognition in New Guinea). A small, black agonine which runs to *Notagonum* in my key to genera of New Guinean Agonini (1952, Part 2, pp. 114–116) but is distinguished by presence of distinct accessory setae on the fifth hind-tarsal segments and by setae on the tips of the ♂ parameres. Length in New Guinea 5.2–6.0 mm.

Occurrence in New Guinea. **West N. G.**: 1, Wissel Lakes, Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.). **N-E. N. G.**: 1, Wau, 1200 m, Sept. 26–27, 1964 (Sedlacek), m. v. light trap; 4, Okapa, June 12, 16, Sept., 1964 (Hornabrook); 1, Purosa (near Okapa), 2000 m, Aug. 21, 1964 (Sedlaceks); 2, 13–20 km SE Okapa, 1800–1900 m, Aug. 27, 1964 (Sedlaceks); 1, L. Sirunki, 2600–2900 m, June 15, 1963 (Sedlacek). **Papua**: 1, Mt. Dayman, Maneau Rge., 2230 m, "N. Slope N. 4," May 19–June 19, 1953 (Geoffrey M. Tate, AMNH).

Notes. At the British Museum in March, 1968, I compared a ♂ *ceylanicum* from Ceylon with the ♂ type of *philippinense* Jedlicka and found no characters to distinguish the latter, and I have compared these with New Guinean specimens and also with Tanaka's excellent description and figures of the unique type of *karasawai*. My conclusion is that all the specimens concerned are probably referable to *ceylanicum*. However, this conclusion is tentative. My material is inadequate for a final study either of the synonymy or of the geographic variation of the species. If my tentative conclusion is correct, *Agonum* (*Sericoda*) *ceylanicum* is now known from Ceylon, Burma, Japan, Sumatra, Borneo, the Philippines (Mindanao, Luzon), and New Guinea.

The fact that *ceylanicum* is so widely distributed on New Guinea at moderate and high altitudes suggests that it has reached the island naturally, by island-hopping (or more properly mountain-hopping) across the Malay Archipelago.

Genus NOTAGONUM Darlington

Darlington 1952, Part II, pp. 115, 127.

Diagnosis (*revised*). Small or medium-sized (4.8–10.0 mm); form *Agonum*-, *Platynus*-, or *Bembidion*-like; never brightly colored, usually not or not strongly iridescent; wings full (except in *ambulator*, *q. v.*); with 2 pairs supraocular and 2 pairs lateral prothoracic setae and 3 dorsal punctures on 3rd elytral intervals; elytral apices simple, denticulate, or spined; tarsi slender, 5th segments without obvious accessory setae; otherwise in general without unusual or striking characters.

Notes. In 1952, I assigned 25 species and 5 additional subspecies of relatively unspecialized New Guinean Agonini to this "genus of convenience." One previously known Australian and 6 new species are added to the number now. Three species described by Maindron and listed by me (Part II, pp. 129–130) as "not identifiable from description" have now been seen (the types, at Paris); they are all slightly different from anything described by me, but the differences are hardly more than subspecific; these species are listed and discussed below, but are not included in the totals given above or in the statistical analyses of the New Guinean carabid fauna in preceding pages. Five other specimens of *Notagonum* have been seen that I cannot place satisfactorily but that are not distinct enough to describe now. This whole genus obviously needs third-stage taxonomic study. A new key to the species seems unnecessary now, but I have keyed out the 4 members of the "*reversum* group" (*q. v.*).

Species of *Notagonum* are now known to be diverse at middle altitudes in New Guinea as well as in the lowlands. Eight have been found at or near Wau (see under

individual species below), and others may occur there. (I found 12 species at Dobodura.)

Notagonum albertisi (Maindron)

Darlington 1952, Part II, p. 130 (*Colpodes*).

Description (*revised*). Form and characters *c.* as in *vile* Darlington. *Head* 0.84 width prothorax. *Prothorax*: lateral margins slightly translucent; sides sinuate, with posterior angles relatively well defined (much better defined than in *novae-guineae*) and baso-lateral impressions punctate roughened (more than in *novae-guineae*). *Lower surface*: abdomen with a little pubescence at extreme base (just a few, sometimes only one or two hair-bearing punctures near middle of base). *Legs*: 4th hind-tarsal segments with good lobes, outer lobe longer than inner. *Length* 7.6–8.4 mm.

Types. From "Fly River, L. M. D'Albertis 1876–77"; 3 examples in Maindron Coll., Paris Mus. (seen); and 14 additional specimens (not types) with same data in Paris Mus. and MCZ.

Notes. This is close to or the same as the species that I have described as *N. vile* (1952, Part II, p. 135) but has a slightly narrower head and a less pubescent abdomen than typical examples of *vile*. I think populations of this species (if it is all one species) in different parts of New Guinea are distinguishable, but they need much more study than I can give them now. In the meantime, I do not care to state synonymy or to designate a lectotype for *albertisi*.

Notagonum novae-guineae (Maindron)

Darlington 1952, Part II, p. 130 (*Colpodes*).

Description (*revised*). Form and characters *c.* of *N. vile* Darlington. *Head* 0.84 width prothorax (minimum width for *vile*). *Prothorax* with lateral margins moderately translucent; side sinuate near base, posterior angles blunted, baso-lateral impressions scarcely punctate. *Elytra* scarcely impressed; subapical sinuations well defined; apices simple; striae slightly punctulate. *Lower surface*: abdomen inconspicuously or perhaps not pubescent even at base. *Legs*: 4th hind-tarsal segment with very short lobes, outer lobes slightly longer than inner. *Length* 6.5 mm.

Type. A single ♀ labeled "B. Jamour [?] . . . 12.VIII. 1903"; in Maindron Coll., Paris Mus. (seen).

Notes. This too (like *albertisi*, above) is apparently an earlier name for *Notagonum vile* Darlington, but (for reasons given in *Notes* under *albertisi*) I am not ready to state the synonymy formally.

Notagonum laglaizei Maindron

Darlington 1952, Part II, p. 130.

Description (*revised*). An ordinary, *Agonum*-like *Notagonum*. *Head* 0.73 width prothorax. *Prothorax* with lateral margins somewhat (not strongly) translucent; sides scarcely sinuate posteriorly; basal angles obtuse; baso-lateral foveae not distinctly punctate. *Elytra* not impressed; subapical sinuations distinct; apices obtusely (slightly) angulate, with sutural angles dentate; striae not distinctly punctate. *Lower surface*: abdomen not pubescent. *Legs*: 4th hind-tarsal segments with moderate lobes, outer lobe longer than inner. *Length* 7 mm.

Type. A single ♂, labeled "Timmena, 6. IV [IX ?] 1904."; in Maindron Coll., Paris Mus. (seen).

Notes. This is probably the species described by me as *Notagonum dentellum* (1952, Part II, p. 147), but the latter is a variable species, and I do not like to state the synonymy without thorough restudy of all available material, which I can not undertake now.

Notagonum submetallicum (White)

White 1846, Voyage Erebus and Terror, Ent., p. 2 (*Colpodes*).

Csiki 1931, Coleop. Cat., Carabidae, Harpalinae 5, p. 873 (see for synonymy and additional references).

Darlington 1963, Breviora (Museum Comparative Zoology) No. 183, pp. 2, 3, figs. 5 (4th hind-tarsal segment), 7 (elytral apex).

Description (for recognition only). With characters of genus; large, rather slender; brown, faintly metallic; not strongly shining, entire upper surface microreticulate, the meshes *c.* isodiametric or only weakly transverse even on elytra; head less than 0.80 width prothorax, with eyes normal; elytra with outer-apical angles not defined, apices *c.* rounded, not distinctly denticulate; 4th hind-tarsal segments emarginate, not lobed; length *c.* 9.5–10.0 mm.

Type. From **Australia**; present location unknown.

Occurrence in New Guinea. **West N. G.**: 4, Wissel Lakes: Itouda, Kamo Vy., 1500 m, Aug. 14, 1955 (Gressitt); Waghete, Tigi L., 1700 m, Aug. 16, 1955 (Gressitt), light trap; L. Paniai, 1750 m, 1939 (H. Boschma, Leiden Mus.); Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.). Also 1, Wamena, 1700 m, Feb. 10–25, 1960 (T. C. Maa, Bishop Mus.).

Notes. In my key to species of *Notagonum* of New Guinea (Part II, pp. 130ff) this runs to couplet 13 but fits neither species there named, differing from *altum* Darlington in having the elytra not more than usually narrowed toward base, and from *sigi* Darlington in being heavily microreticulate. It is in fact probably not directly related to either of these species.

N. submetallicum is very common in southern temperate Australia, where it is found in a variety of wet places. It occurs much more rarely northward in eastern Australia into the subtropics and tropics: I found it near Brisbane, and on the Atherton Tableland at near 1000 m altitude in grass growing over cool running water (Darlington, 1963). Its occurrence in *West* rather than eastern New Guinea is, however, surprising.

Although there may be slight differences between New Guinean and Australian individuals, I do not wish to describe a New Guinean subspecies. Comparison of the copulatory organs of a ♂ from Brisbane, Australia, and a ♂ from Wissel Lakes, New Guinea, shows only slight differences which may be individual rather than geographic. The species needs study as a whole, including statistical analysis of population samples from different parts of Australia, before its status in New Guinea can be settled. This is third-stage taxonomy, which I cannot undertake now.

Notagonum angustellum Darlington

Darlington 1952, Part II, pp. 130, 133.

Additional material. Ninety-six, from widely scattered localities including the following. **Papua**: 2, Owen Stanley Rge., Goilala: Tapini, 975 m, Nov. 16–25, 1957 (W. W. Brandt, Bishop Mus.). **N-E. N. G.**: 50, Wau, 1100, 1200, 1300 (1 only), 1500 (1 only), dates in Mar., Apr., May, July, Aug., Sept., Nov., Dec., 1961–1966 (Sedlaceks and others); 14, Finisterre Rge., Moro, Stn. No. 85, *c.* 5550 ft. (*c.* 1700 m), Oct. 30–Nov. 15, 1964 (Bacchus, British Mus.). **West N. G.**: 11, Star Rge., various localities, 1260, 1300, 1500 m, dates in May, June, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. Although this species occurs at low altitudes (for example at Dobodura) as well as in the mountains, it lives only (in my experience) on the banks of small, rapidly flowing streams, and this habitat restriction may retard its dispersal. Detailed taxonomic study of available material would probably show that it varies geographically within the limits of New Guinea.

Notagonum subnigrum Darlington

Darlington 1952, Part II, pp. 130, 134.

Additional material. **Papua**: 21, Mt. Lamington, 500 m, June 1966 (P. Shanahan, Bishop Mus.); 1, Biniguni, Gwariu R., 150 m, "No. 3," July 27–Aug. 14, 1953 (Geoffrey M. Tate, AMNH); 67, Peria Ck., Kwagira R., 50 m, "No. 7," Aug. 14–Sept. 6, 1953 (Geoffrey M. Tate, AMNH).

Notes. This species is very distinct from populations of other species in eastern New Guinea, but its relationships with western New Guinean forms are undetermined (see *Notes* under original description).

Notagonum vile Darlington

Darlington 1952, Part II, pp. 130, 135.

Additional material. One hundred and sixty-eight, from all three political divisions of New Guinea, including 33 from Wau & vic., 1050, 1200, 1250, 1200–1300, 1500, 1500–1900, 1600 m, Feb., Mar., Apr., May, June, Aug., Sept., Oct., Nov., 1961–1966 (Sedlaceks and others).

Notes. This material, and that recorded by me in 1952, should be sufficient for third-stage taxonomic study of the geographic variation of this species within New Guinea. Such variation obviously does occur, but I cannot undertake to analyze it now. (See also *N. albertisi* and *novae-guineae*, previous pages.)

Notagonum Reversum Group

The four species keyed out below form what may be called the *reversum* group of *Notagonum.* They share the following characters: head usually more than 0.85 width prothorax, with eyes usually (not always) abruptly prominent; prothorax with sides usually sinuate well before base; elytra with humeri obtusely angulate or subangulate, with subapical sinuations weak or absent, and apices simply rounded except often denticulate at suture; abdomen not pubescent. The group is notable for occurring at relatively high altitudes, compared with most other members of the genus. One of the species, *N. ambulator* (below), is the first known *Notagonum* with atrophied wings, but is so obviously closely related to the winged forms that it cannot be ruled out of the genus.

Key to Species of Notagonum Reversum Group

1. Eyes normal; base of prothorax not punctate .... *reversum*
– Eyes more abruptly prominent; base of prothorax conspicuously punctate 2
2. Prothorax with sides sinuate *c.* ⅓ of length before base .... *reversior*
– Sides of prothorax sinuate nearer base 3
3. Winged; length 9.7 mm .... *curiosum*
– Wings atrophied; length *c.* 7.8 mm .... *ambulator*

Notagonum reversum Darlington

Darlington 1952, Part II, p. 136.

Notes. Still known only from the type series from the Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5000–7000 ft. (*c.* 1500–2300 m).

Notagonum reversior Darlington

Darlington 1952, Part II, p. 137.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 2800–2900 m, July 6, 1963 (Sedlacek).

Notes. The 2 types were from Moss Forest Camp, Snow Mountains, **West N. G.**, 2800 m. The individual recorded above is apparently referable to this species, although further material may show that it is a geographic form distinguishable by slightly different proportions, etc.

Notagonum curiosum n. sp.

Description. With characters of genus and of *reversum* group; form as in Figure 28, slender, appendages slender; brown, head and pronotal disc darker, appendages reddish testaceous; moderately shining, reticulate microsculpture faint on front and pronotum, distinct and transverse on elytra. *Head* 0.87 width prothorax; eyes small, more abruptly prominent than usual (but less so than in *reversum*). *Prothorax*: width/length 1.11; base/apex 1.27; base and apex deeply margined; lateral margins narrow, subangulate at median-lateral setae, strongly sinuate *c.* ⅕ from base, with posterior angles sharply formed, *c.* right; disc convex, middle line distinct, anterior impression not sharply defined, posterior transverse impression deep, baso-lateral impressions small; entire base of pronotum punctate. *Elytra*: width elytra/prothorax 1.65; base margined, margin subangulate at humeri; subapical sinuations obsolete; apices apparently broadly rounded (slightly broken) except angulate or vaguely subdentate at suture; striae impressed, not punctulate; intervals *c.* flat. *Inner wings*

fully developed. *Lower surface*: sides of sterna in part punctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate, scarcely lobed. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length 9.7 mm; width 3.3 mm.

Type. Holotype ♂ (Bishop Mus.) from Owen Stanley Rge., **Papua**, Goilala, Bome, 1950 m, Mar. 16–31, 1958 (W. W. Brandt); the type is unique.

Notes. For comparisons, see preceding *Key to Species of Reversum Group*.

Notagonum ambulator n. sp.

Description. With characters of genus and of *reversum* group, except wings atrophied; form as in Figure 29, elytra more narrowed basally than usual; brown, head and pronotal disc darker, appendages yellow; moderately shining, reticulate microsculpture faint on head, very light and transverse on pronotum; irregularly transverse on elytra. *Head* 0.87 and 0.84 width prothorax; eyes small but more abruptly prominent than usual, with posterior supraocular setae behind posterior eye level. *Prothorax*: width/length 1.15 and 1.15; base/apex 1.16 and 1.23; base and apex margined; sides broadly sinuate well before base, with basal angles sharply formed, *c*. right or slightly acute; lateral margins very narrow; disc convex, with middle line and anterior transverse impression normal, posterior transverse impression deeper (in the type), and baso-lateral impressions small but rather deep; whole basal area strongly punctate. *Elytra*: width elytra/prothorax 1.60 and 1.55; base margined, margin faintly subangulate at humeri; subapical sinuations slight or obsolete; apices independently rounded then sinuate to denticulate sutural angles; striae deep, not punctulate; intervals convex. *Inner wings* atrophied, reduced to vestiges *c*. ⅓ as long as elytra. *Lower surface*: sides of pro- and mesosterna punctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate, with very short lobe on outer side. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c*. 7.8; width 2.7–2.8 mm.

Types. Holotype ♀ (CSIRO) from Murmur Pass (W of Mt. Hagen), **N-E. N. G.**, 8600 ft. (*c*. 2620 m), Nov. 1961 (W. W. Brandt); and 1 ♀ paratype (Bishop Mus.), 32 km E Wapenamanda (Western Highlands), **N-E. N. G.**, 2500–2700 m, June 9, 1963 (M. Sedlacek).

Notes. Although evidently related to *N. reversior* (Darlington 1952, Part II, p. 137), this species seems distinct by prothorax much less sinuate with the sinuations nearer base, as well as by atrophy of wings. These differences may conceivably all be due to a single mutation, but I cannot assume this without further evidence, and the occurrence of a short winged species of *Notagonum* is worth recording now.

Notagonum externum Darlington

Darlington 1952, Part II, pp. 131, 138.

Additional material. **Papua**: 2, Popondetta, 25 m, June 1966 (Shanahan-Lippert, Bishop Mus.), light trap; 1, Mt. Lamington, 1300–1500 ft. (*c*. 400–450 m) (C. T. McNamara, South Australian Mus.).

Notagonum sigi Darlington

Darlington 1952, Part II, pp. 131, 143.

Additional material. **N-E. N. G.**: 3, Wau, 1100 m, Sept. 9, 1961 (Sedlacek).

Notes. *N. sigi* is superficially very much like *vile* but lacks the sparse but distinct ventral pubescence of *vile* and has a slightly narrower prothoracic base, although the proportions of both species vary and may overlap. The fact that the three Wau individuals were all taken at one time and place suggests that they came from one particular habitat, while *vile* is apparently much more widely distributed altitudinally and perhaps ecologically.

Notagonum sinuum Darlington

Darlington 1952, Part II, pp. 131, 139.

Additional material. **Papua**: 1, Biniguni,

Gwariu R., 150 m, "No. 3," July 27–Aug. 14, 1953 (Geoffrey M. Tate, AMNH). **N-E. N. G.**: 1, Adelbert Mts., Wanuma, 800–1000 m, Oct. 24, 1958 (Gressitt); 1, Finisterre Rge., Budemu, Stn. No. 51, *c.* 4000 ft. (*c.* 1220 m), Oct. 15–24, 1964 (Bacchus, British Mus.); 2, Herzog Rge., Vagau, Stn. No. 137, 147A, *c.* 4000 ft. (*c.* 1220 m), Jan. 4–17, 1965 (Bacchus, British Mus.).

Notes. This species, now known from all three political divisions of New Guinea, occurs chiefly at moderate altitudes in the mountains, but evidently descends to or nearly to sea level.

Notagonum altum Darlington

Darlington 1952, Part II, pp. 131, 144.

Additional material. **N-E. N. G.**: 4, Mt. Wilhelm, 2800–2900 m, July 6, 1963 (Sedlacek); 2, Sarua Kup, Kubor Rge., Oct. 31, 1965 (Dept. Agr. Port Moresby); 6, Finisterre Rge., S side Mt. Abilala, Stn. No. 100, 8000 ft. (*c.* 2440 m), Nov. 17, 1964 (Bacchus, British Mus.).

Notagonum margaritum Darlington

Darlington 1952, Part II, pp. 131, 145.

Additional material. One hundred one, from all three political divisions of New Guinea, including the following. **N-E. N. G.**: 16, Wau & vic. (incl. Mt. Missim, Mt. Kaindi), 1100, 1150, 1200, 1250, 1600–1650, 1800, 2300 m, dates in Jan., Feb., May, June, Sept., Oct., Dec., 1961–1966 (Sedlaceks and others). **West N. G.**: 60, Star Rge., various localities, 1260, 1300, 1500 m, dates in May, June, July, Aug., 1959 (Leiden Mus., Neth. N. G. Exp.), many at light including ultraviolet light; 1, Waigeu Is., Camp Nok, 2500 ft. (*c.* 760 m), Apr. 1938 (Cheesman).

Notes. This species is apparently common over an exceptionally wide altitudinal range, from near sea level in some cases (see localities given in 1952) to middle altitudes in the mountains.

Notagonum subpunctum Darlington

Darlington 1952, Part II, pp. 131, 146.

Additional material. **Papua**: 10, Kiunga, Fly R., dates in July, Aug., Sept. 1957 (W. W. Brandt, Bishop Mus.); 1, Kokoda, 360 m, Mar. 20, 1956 (Gressitt), light trap; 1, Mamoo Plantation, Northern Dist., Mar. 22, 1956 (Dept. Agr. Port Moresby), at light. **N-E. N. G.**: 2, Minj, Western Highlands, 5200 ft. (*c.* 1600 m) May 20, 1960 (J. H. Barrett, Dept. Agr. Port Moresby), at m. v. lamp. **West N. G.**: 1, Star Rge., Sibil, 1260 m, June 16, 1959 (Leiden Mus., Neth. N. G. Exp.), at light.

Notes. This species, including subspecies *capitis* Darlington (1952: 147), is now known from nearly the whole length of New Guinea, from sea level to moderate altitudes in the mountains. However, it has not yet been found in the Morobe area.

The specimens from the Fly River represent a population which, in size and elytral microsculpture, is more like subspecies *capitis* from the Vogelkop than like typical *subpunctum* from Dobodura (northern Papua) etc., but which differs slightly from *capitis* in form of elytral apices, which are usually a little more distinctly angulate than in *capitis*. However, extremes of the two forms are hardly distinguishable. I do not wish to describe a Fly River form now, but mention it as an example of geographic variation at low altitudes within New Guinea. This kind of local geographic variation will probably be found to occur in many other lowland carabids when adequate series from different parts of the island are available.

Notagonum dentellum Darlington

Darlington 1952, Part II, pp. 132, 147.
——— 1963, Breviora (Museum of Comparative Zoology), No. 183: 3, 5.

Additional material. Twelve, from all three political divisions of New Guinea and Goodenough Island, including the following localities. **N-E. N. G.**: 1, Bulolo (Morobe area), 730 m, Aug. 31, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Western Highlands: Baiyer, 1150 m, Oct. 19, 1958 (Gressitt), light trap; 1, Torricelli Mts., Mobitei, 750 m,

Apr. 1–15, 1959 (W. W. Brandt, Bishop Mus.).

Notes. This variable species is widely distributed in New Guinea at low and moderate altitudes (subspecies *chimbu* Darlington (1952: 149) is on the Bismarck Range at at least 5000 ft. (*c.* 1525 m)) and occurs also in tropical northern **Australia**.

Notagonum subimpressum Darlington

Darlington 1952, Part II, pp. 132, 149.

Additional material. Eleven, from all three political divisions of New Guinea and Fergusson Is.; none above 500 m (previous highest record, 800 m, in Snow Mts.); 1, Sangeman Village, nr. Busu R., NE of Lae, 25 m, Aug. 30, 1957 (D. Elmo Hardy, Bishop Mus.), at light; not found near Wau.

Notagonum paludum Darlington

Darlington 1952, Part II, pp. 132, 150.

Additional material. **Papua**: 1, Popondetta, 25 m, May 1966 (Shanahan-Lippert, Bishop Mus.); 1, Normanby Is., Wakaiuna, Sewa Bay, Nov. 11–20, 1956 (W. W. Brandt, Bishop Mus.).

Notagonum addendum Darlington

Darlington 1952, Part II, pp. 132, 153.

Additional material. **West N. G.**: 5, Waigeo Is., Camp Nok, 2500 ft. (*c.* 760 m), April 1938 (Cheesman). These specimens are in addition to 2 paratypes from the same locality recorded in 1952.

Notes. For comments on the relation of this species to *Altagonum vallicola*, see the latter, below.

Notagonum angulum Darlington

Darlington 1952, Part II, pp. 132, 154.

Additional material. **West N. G.**: 5, Star Rge., various localities, 1260, 1300, 1500, 1800 m, dates in May, June, July 1959 (Leiden Mus., Neth. N. G. Exp.); 1, Wissel Lakes, Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.); 1, Bokondini, 40 km N of Baliem Valley, *c.* 1300 m, Nov. 16–23, 1961 (no collector given), Malaise trap. **N-E. N. G.**: 20, Wau and vic. (Mt. Missim, Mt. Kaindi, Nami Ck., Edie Ck., Bulldog Rd.), 1100, 1200, 1250, 1700, 2000, 2200, 2300, 2350 m, Jan., Feb., May, June, Aug., Sept., Oct., Nov., Dec. 1961–1965 (Sedlaceks), some at light including m. v. light, also in Malaise trap; 8, same area (Edie Ck. and Mt. Kaindi), Stn. No. 10, 20, 7000, 8000 ft. (*c.* 2135, 2440 m), Sept. 17, 22, 1964 (Bacchus, British Mus.); 2, Feramin, 1200–1500 m, May 11–22, 23–31, 1959 (W. W. Brandt, Bishop Mus.); 1, Swart Vy., Karubaka, 1450 m, Nov. 12, 1958 (Gressitt), light trap; 3, Okapa, May, June, 1965 (Hornabrook); 2, same locality, Stn. No. 170, *c.* 5000 ft. (*c.* 1525 m), Feb. 4–15, 1965 (Bacchus, British Mus.); 1, Wonenara, nr. Kratke Mts., 1450 m, June 14, 1966 (Gressitt), light trap; 1, 11 km S of Mt. Hagen (town), 2000–2300 m, May 20, 1963 (Sedlacek); 1, Sarua Kup, Kubor Rge., Oct. 31, 1965 (Dept. Agr. Port Moresby); 8, Finisterre Rge., Budemu and Moro, Stn. No. 51, 78, 4000, 5500 ft. (*c.* 1220, 1675 m), Oct. 15–24, Oct. 30–Nov. 15, 1964 (Bacchus, British Mus.). **Papua**: 1, Owen Stanley Rge., Goilala: Tapini, 975 m, Nov. 16–25, 1957 (W. W. Brandt, Bishop Mus.).

Notes. The occurrence of this very distinct species seems worth giving in full, as an example of the distribution of a widely spread but strictly mountain living New Guinean carabid.

Notagonum subrufum Darlington

Darlington 1952, Part II, pp. 133, 156.

Additional material. **N-E. N. G.**: 1, Finisterre Rge., Moro, *c.* 5550 ft. (*c.* 1690 m), Oct. 30–Nov. 15, 1964 (Bacchus, British Mus.).

Notes. This very distinct species has been previously known only from two specimens from Rattan Camp, Snow Mts., **West N. G.**, at 1200 m.

Notagonum subspinulum Darlington

Darlington 1952, Part II, pp. 133, 158.

Additional material. **Papua**: 1, Goodenough Is., "E. Slope No. 10," 900 m, Oct. 24–30, 1953 (Geoffrey M. Tate, AMNH); 1, Mt. Riu, Sudest Is., "No. 10," 250–350 m, Aug. 22, 1956 (L. J. Brass, AMNH). **N-E. N. G.**: 1, "Krisa, N. New Guinea, Vanimo," Apr. 1939 (Cheesman, South Australian Mus.).

Notagonum astrum n. sp.

Description. With characters of genus; form as in Figure 30; black, legs bicolored (femora dark at base pale at apex, tibiae dark, tarsi pale with small black spots at articulations), antennae dark with basal segment pale; moderately shining, reticulate microsculpture light, isodiametric on front, transverse on pronotum and elytra. *Head* 0.88 width prothorax; eyes large, normal. *Prothorax*: width/length 1.39; base/apex 1.18; sides rounded almost to base, then slightly sinuate before very obtuse, narrowly rounded posterior angles; lateral margins narrow; baso-lateral impressions small, vaguely punctate; base indistinctly, apex not margined at middle; disc convex, with distinct middle line, indistinct or irregular transverse impressions. *Elytra*: width elytra/prothorax 1.72; margins broadly rounded at humeri; subapical sinuations weak; apices narrowly independently rounded; striae impressed, outer (not inner) ones slightly punctulate; intervals slightly convex. *Lower surface* not punctulate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment strongly lobed, outer lobe longer than inner. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length 8.0 mm; width 3.1 mm.

Type. Holotype ♂ (Leiden Mus.) from Star Rge., **West N. G.**, 1300 m, "Bivak 39," June 28, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. In my key to species of *Notagonum* (Part II, pp. 130ff) this new species runs to couplet 2 but fits neither part of the couplet, the sides of the prothorax being sinuate relatively near the base but the abdomen not being pubescent. The new species may actually be most closely related to *N. gibbum* (couplet 12) but has a wider head and bicolored legs, the latter distinguishing the present species from any other *Notagonum* known to me.

Notagonum exactum n. sp.

Description. With characters of genus; form as in Figure 31, with elytra more oval than usual (but inner wings long and folded); brownish black, lateral margins of elytra and (less distinctly) of prothorax narrowly testaceous, appendages testaceous except antennae browner from 4th segments; shining, elytra subiridescent, reticulate microsculpture light and so strongly transverse on elytra as to be scarcely distinguishable. *Head* 0.82 width prothorax; eyes normal. *Prothorax* cordate; width/length 1.39; base/apex 1.07; lateral margins moderate; posterior angles right and exactly defined; base margined, apex not margined at middle; disc normal, baso-lateral impressions moderately deep, vaguely subpunctate, and base slightly longitudinally wrinkled at middle. *Elytra* quadrate-suboval, each slightly (independently) impressed before middle; width elytra/prothorax 1.64; subapical sinuations moderate; apices subtruncate with sutural angles very briefly dehiscent and weakly subdentate; striae impressed, slightly irregular but not distinctly punctulate; intervals slightly convex. *Lower surface* c. impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segments rather strongly lobed, outer lobe longer than inner. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length 6.7 mm; width 2.6 mm.

Type. Holotype ♂ (Bishop Mus.) from Wau, Morobe Dist., **N-E. N. G.**, 1200 m, July 16–22, 1962 (M. Sedlacek); the type is unique.

Notes. In my key to the species of *Notagonum* (Part II, pp. 130ff) this runs to *dentellum*, but the present species has the posterior angles of prothorax much better defined and the elytra more oval. The dif-

ference in shape of prothorax is striking on comparison of specimens.

Notagonum quadruum n. sp.

Description. With characters of genus; form as in Figure 32, rather depressed, elytra impressed near or slightly before middle; black, lateral margins of prothorax and elytra narrowly testaceous-translucent, appendages testaceous except antennae slightly darker except at base; shining, reticulate microsculpture absent or faint on front and disc of pronotum, light but distinct and strongly transverse on elytra. *Head* 0.76 and 0.75 width prothorax; eyes normal. *Prothorax*: width/length 1.45 and 1.49; base/apex 1.11 and 1.09; lateral margins moderate and moderately reflexed; apex finely margined, base not or indistinctly so; disc with usual impressions, impunctate except vaguely subpunctate in baso-lateral impressions. *Elytra*: width elytra/prothorax 1.51 and 1.53; subapical sinuations strong; apices acutely angulate then emarginate to acutely denticulate (almost spined) sutural angles; striae impressed, not distinctly punctulate; intervals slightly convex. *Lower surface* not or not much punctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment rather strongly lobed, outer lobe longer than inner. *Measurements*: length 8.2–9.8 mm; width 3.2–3.7 mm.

Types. Holotype ♂ (Bishop Mus.) and 9 paratypes (some in MCZ, Type No. 31822) from Wau, Morobe Dist., **N-E. N. G.**, 1200 (1 paratype 1200–1300) m, dates in Mar., Apr., Oct., 1961–1964 (holotype, Oct. 11, 1962) (Sedlaceks); and 1 additional paratype from Wau, 3400 ft. (slightly over 1000 m), "3.8.62" (J. J. H. Szent-Ivany, Dept. Agr. Port Moresby).

Additional material. **Papua**: 1, Tapini, (Owen Stanley Rge., *c.* 1200 m), May 17–19, 1961 (Gressitt). **N-E. N. G.**: 1, Torricelli Mts., Mobitei, 750 m, Mar. 16–31, 1959 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Star Rge., Sibil, 1260 m, June 16, 1959 (Neth. N. G. Exp., Leiden Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Wau, 1200 m.

Notes. In my key to species of *Notagonum* (Part II, pp. 130ff), the present new species runs to *margaritum* Darlington (couplet 20) but has elytral denticles much more prominent than *margaritum*, elytral striae not punctulate, and differs in other ways. The individual from the Torricelli Mts. has dark rather than pale legs and may represent an independent population.

Some of the specimens recorded above were taken in light traps including mercury vapor light traps.

Notagonum sectum n. sp.

Description. With characters of genus; form as in Figure 33, with elytra independently impressed *c.* ⅔ from apex; black, lateral margins prothorax and elytra narrowly slightly translucent, appendages dark; moderately shining, reticulate microsculpture in part light or indistinct on head and pronotum, more distinct and transverse on elytra. *Head* 0.72 width prothorax; eyes large, normal. *Prothorax* wide-subcordate; width/length 1.45; base/apex 1.24; lateral margins rather wide; apex margined, base faintly margined; disc weakly convex, basolateral impressions moderate, poorly defined, irregular but scarcely punctate. *Elytra* long-subquadrate, width elytra/prothorax 1.46; apices strikingly modified, with outer-apical angles *c.* right and sharply defined, each apex then strongly emarginate to second angulation *c.* opposite end 3rd stria, then again emarginate to moderate spine at sutural angle; striae moderately impressed, slightly irregular but not punctulate; intervals flat or slightly convex. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segments moderately lobed, outer lobe longer than inner. *Measurements*: length 9.8 mm (including spines); width 3.6 mm.

Type. Holotype ♀ (Bishop Mus.) from Mokai Village, Torricelli Mts., **N-E. N. G.**, 750 m, Dec. 8–15, 1958 (W. W. Brandt); the type is unique.

Notes. Although based on a single fe-

male, this species is so strikingly characterized by form of elytral apices that it is worth describing. In my key to the species of *Notagonum* (Part II, pp. 130ff) it runs to *N. externum* (couplet 7) because the outer-apical elytral angles are sharply defined, but the elytral apices are otherwise much more modified than in *externum*. These two species are probably not directly related.

Genus *VIOLAGONUM* Darlington

Darlington 1956, Psyche 63, p. 8.

Diagnosis and *description*. See reference given.

Type species. Colpodes violaceus Chaudoir.

Generic distribution. See following *Notes*.

Notes. This genus of medium-sized Agonini is distinguished from *Colpodes* by shorter head, and from *Notagonum* by position of elytral spines. The principal species of the genus is *V. violaceum* (Chaudoir), which occurs in **New Guinea**, **New Britain**, the **Solomons**, and **NE Australia**, with subspecies *goa* Louwerens (1956, Treubia, 23: 221, 231) in the **Moluccas**. *V. ("Colpodes") piceus* (Andrewes) represents the group on ***Samoa***. And an undescribed species occurs on the **Palau Islands** (Darlington, 1970: 23).

Violagonum violaceum (Chaudoir)

Colpodes violaceus auct. including Darlington 1952, Part II, pp. 159, 160.

Additional material. Two hundred sixty-eight, from all three political divisions of New Guinea and Goodenough, Normanby, Woodlark, Rossel, Fergusson, Sudest, and Biak Is., and including the following. **N-E. N. G.**: 126, Wau and vic., altitudes from 1050 to 1700–1800 m (most from 1050 to 1300 m), dates in every month, 1961–1963 (Sedlaceks), some at light, some in Malaise trap. **Papua**: 2, Mt. Giluwe, 2500, 2550 m, May 1, May 27–June 6, 1963 (Sedlacek). **West N. G.**: 4, Star Rge., various localities, 1220, 1260, 1500 m, dates in May, July, Aug. 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. This is one of the commonest Carabidae in New Guinea. It evidently occurs throughout the island from sea level to moderate altitudes in the mountains, and rarely at higher altitudes. It is easily recognized by its rather broad form, size (length *c.* 10 mm), purple or blue color, and elytra each with a single, moderate apical spine *c.* opposite the end of the second interval. It is partly arboreal, occurring in vegetation including clumps of leaves on low branches in rain forest and also in piles of dead leaves on the ground in forest. It often flies to light.

Genus *COLPODES* Macleay

Darlington 1952, Part II, pp. 115, 158.

Notes. As I (and many other authors) have used it, this is a "genus of convenience" to which can be referred relatively large, usually tropical Agonini not now referable to more exactly defined generic groups. The single new species described below is probably not directly related to any previously known New Guinean "*Colpodes*" but may be independently derived from *Notagonum*.

Colpodes guega n. sp.

Description. With characters of genus as restricted (Part II, pp. 158–159); form as in Figure 34; dark brown with lateral margins of prothorax and (less distinctly) of elytra translucent, appendages paler; moderately shining, reticulate microsculpture faint and *c.* isodiametric on front, light and strongly transverse on pronotum, still more strongly transverse on (faintly iridescent) elytra. *Head* 0.74 width prothorax; eyes normal; front not wrinkled. *Prothorax*: width/length 1.39; base/apex 1.41; lateral margins moderate; apex strongly margined, base very narrowly indistinctly so; disc convex, middle line distinct, transverse impressions slight; baso-lateral impressions poorly defined, not distinctly punctate. *Elytra*: width elytra/prothorax 1.47; base margined, margin rounded-obtuse at humeri; apices

with outer angles not defined, subapical sinuations broad, actual apices acutely angulate *c.* opposite ends 3rd intervals and obtusely angulate (almost minutely denticulate) at suture; striae moderately impressed, not distinctly punctulate; intervals slightly convex, 3rd 3-punctate as usual, 8th and 9th not specially modified at apex. *Lower surface* *c.* impunctate, without special pubescence. *Legs*: 4th hind-tarsal segments lobed, outer lobe longer than inner. *Secondary sexual characters*: ♀ with only 1 seta-bearing puncture each side apex last ventral segment; ♂ unknown. *Measurements*: length 11.5; width 4.3 mm.

Type. Holotype ♀ (sex determined by dissection) (Bishop Mus.) from Guega, W of Swart Valley, **West N. G.**, 1200 m, Nov. 14, 1958 (Gressitt); the type is unique.

Notes. In my key to *Colpodes* of New Guinea (Part II, pp. 159–160), this runs to couplet 9 but fits neither half of the couplet, differing from *acuticauda* in having elytra with entire basal margins and elytral 3rd intervals 3-punctate, and differing from *sinuicauda* and *simplicicauda* in having elytral apices conspicuously angulate. See also *Notes* under genus, above.

Colpodes saphyrinus sloanei Maindron

Darlington 1952, Part II, pp. 160, 161.

Additional material. **West N. G.**: 1, Star Rge., Bivak 39A, 1500 m, July 3, 1959, and 1, Star Rge., Sibil, 1260 m, June 21, 1959 (both Netherlands-New Guinea Exp., Leiden Mus.); 1, Waigeu Is., Camp Nok, 2500 ft. (660 m), Apr. 1938 (Cheesman). **N-E. N. G.**: 52, Wau, 980–1100, 1200, 1250, 1300, 1200–1500 m, Jan. (most), Feb., Mar., May, Aug., Sept., Oct., Dec., 1961–1964 (Sedlaceks), some in light traps; 1, Mt. Kaindi, 1000 m, July 9, 1963 (Sedlaceks); 1, Karimui, 1080 m, July 11–12, 1963 (Sedlacek); 5, Eliptamin Vy., 1200–1350, 1350–1665, 1665–2530 m, June, Aug., Sept., 1959 (W. W. Brandt, Bishop Mus.). **Papua**: 1, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.).

Notes. This species is evidently characteristic of the lower mountain slopes in New Guinea. It rarely occurs near sea level (3 at Dobodura, previously recorded) and has rarely been found above 1500 m.

Colpodes helluo Darlington

Darlington 1952, Part II, pp. 160, 162.

Additional material. **West N. G.**: 1, Star Rge., Tenma Sigin, 1800 m, May 20, 1959 (Leiden Mus., Neth. N. G. Exp.), at light (the types came from Rattan Camp in the Snow Mts. at 1150 m). **N-E. N. G.**: 6, Wau, altitudes from 1200–1400–1500 m, Mar., Apr., June, Sept., Dec., 1961–1964 (Sedlacek, Gressitt), 1 taken at light; 9, Eliptamin Vy., 1200–1350 m, dates in June, July, Aug., Sept., 1959 (W. W. Brandt, Bishop Mus.); 5, Okapa & vic., some at 1800–1900 m, Aug. 27, 1964 (Hornabrook and Sedlaceks), some under stones; 3, Wanatabe Vy., nr. Okapa, Stn. No. 174, *c.* 5000 ft. (1525 m), Feb. 5, 1965 (Bacchus, British Mus); 1, Koibuga, E Highlands, 1500 m, July 5, 1963 (Sedlaceks); 1, Finisterre Rge., Budemu, Stn. No. 51, *c.* 4000 ft. (1220 m), Oct. 15–24, 1964 (Bacchus, British Mus.). **Papua**: 2, Owen Stanley Rge., Goilala: Tororo, 1560 m, Feb. 15–20, and Bome, 1950 m, Mar. 8–15, 1958 (W. W. Brandt, Bishop Mus.).

Notes. This very distinct species is easily recognized by form (Fig. 35) and form of elytral apices. It is evidently widely distributed at moderate altitudes in New Guinea.

Colpodes laetus (Erichson)

Darlington 1952, Part II, pp. 160, 163.

Additional material. Seventeen, from all three political divisions of New Guinea; most at low altitudes (usually near sea level) but 1, Wau, 1200 m, Jan. 29, 1963 (Sedlaceks), light trap, and 3, Eliptamin Vy., 1350–1665 and 1665–2530 m, dates in June 1959 (W. W. Brandt, Bishop Mus.).

Notes. *Colpodes laetus laetus* is now known on the **Bonin Is.** as well as the **Philippines**, **Celebes**, **New Guinea** (not Australia), **Solomons**, and **New Hebrides**, and *C. l. pacificus* Andrewes is on **Samoa**

and the **E Caroline Is.** (Kusaie) (Darlington, 1970: 24).

Colpodes habilis Sloane

Darlington 1952, Part II, pp. 160, 164.
——— 1963, Breviora (Museum of Comparative Zoology), No. 183: 5.

Additional material. One hundred thirty-four, from all three political divisions of **New Guinea**, few near sea level, most between 1000 and 2000 m, none specifically higher. Included in this total are 52 from Wau, 1050 to 2000 m, dates in every month, many specimens at light.

Notes. Occurs also on **Buru**, **New Britain**, **Solomons**, and **Santa Cruz Is.**, and in tropical northern **Australia.**

Colpodes bennigseni Sloane

Darlington 1952, Part II, pp. 160, 165.

Additional material. **N-E. N. G.**: 34, Wau & vic., 1200 m (most so labeled, but some without altitude), Feb., Mar., Apr., May, June, July, Aug., Nov., Dec., 1961–1966 (Sedlaceks and others), some in light traps; 1, Okapa, Mar. 20, 1964 (Hornabrook); 4, Eliptamin Vy., 1200–1350, 1665–2530 m, June, July, Aug., 1959 (W. W. Brandt, Bishop Mus.); 1, Torricelli Mts., Mokai Village, 750 m, Dec. 16–31, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 4, Star Rge., Sibil, 1260 m, dates in Apr., May, June, 1959 (Leiden Mus., Neth. N. G. Exp.), some at light.

Notes. This species, like *habilis* (above), occasionally occurs near sea level (see localities cited in 1952) but is mainly characteristic of middle altitudes in the mountains.

Colpodes rex Darlington

Darlington 1952, Part II, pp. 160, 167.

Additional material. **West N. G.**: 11, Star Rge., Bivak 34A at 850 m, Bivak 39A at 1500 m (most), Sibil at 1260 m, dates in May, June, July, Aug., 1959 (Leiden Mus., Neth. N. G. Exp.), at least 1 at light; 6, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman); 7, Waigeu Is., Camp Nok, 2500 ft. (660 m), Apr. 1938 (Cheesman). **N-E. N. G.**: 6, Eliptamin Vy., 1200–1350, 1350–1665, 1665–2530 m, dates in June, July, 1959 (W. W. Brandt, Bishop Mus.); 2, Feramin, 1200–1500 m, June 7–14, 15–18, 1959 (W. W. Brandt, Bishop Mus.); 4, Torricelli Mts., Mobitei & Mokai Village, 750 m, dates in Dec. 1958, Feb., Mar., 1959 (W. W. Brandt, Bishop Mus.); 1, Finisterre Rge., Saidor: Matoko, Aug. 28–Sept. 5, 1958 (W. W. Brandt, Bishop Mus.).

Notes. It is surprising that this striking endemic species, which has been found in all three political divisions of the island (Papuan examples are recorded in 1952), has not been found at Wau or anywhere in the Morobe area. Otherwise the species seems to be widely distributed in New Guinea at moderate altitudes, rarely below 1000 m.

Colpodes acuticauda Darlington

Darlington 1952, Part II, pp. 160, 170.

Additional material. **N-E. N. G.**: 1, Wau, 2500 m, Dec. 28, 1961 (Sedlacek); 1, Finisterre Rge., Saidor, Matoko Village, (*c.* 1500 m), Sept. 6–24, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Star Rge., Bivak 39, June 28, 1959 (Leiden Mus., Neth. N. G. Exp.).

Colpodes sinuicauda Darlington

Darlington 1952, Part II, pp. 160, 171.

Additional material. **N-E. N. G.**: 1, Wau, 1700–1800 m, Oct. 7, 1962 (Sedlaceks); 1, Caves near Telefomin, Aug. 1964 (B. Craig, South Australian Museum). **Papua**: 1, Mt. Dayman, Maneau Rge., 1550 m, N Slope No. 5, June 30–July 13, 1953 (Geoffrey M. Tate, AMNH).

Notes. The 2 types were from Sigi Camp, Snow Mts., **West N. G.**, at 1500 m. This distinct species is therefore now known from all three political divisions of New Guinea, but from a total of only 5 specimens.

Colpodes simplicicauda Darlington

Darlington 1952, Part II, pp. 160, 172.

Additional material. **West N. G.**: 2, Wissel Lakes, Enarotadi, 1550 m, July 25–29, 1962 (Sedlacek) and Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.). **N-E. N. G.**: 11, Wau & vic. (incl. Edie Ck. and Mt. Kaindi), altitudes 1200 to 2400 (most over 2000) m, Jan., May, June, Oct., 1961–1963 (Sedlaceks), some in light traps; 1, 16 km NW of Banz, 1700–2100 m, June 28–29, 1963 (Sedlacek); 1, 32 km E of Wapenamanda, 2500–2700 m, June 9, 1963 (Sedlacek); 1, Finisterre Rge., Saidor, Matoko Village, Sept. 6–24, 1958 (W. W. Brandt, Bishop Mus.). **Papua**: 2, Owen Stanley Rge., Goilala: Bome, 1950 m, Mar. 8–15, 1958 (W. W. Brandt, Bishop Mus.).

Notes. This species too, like several of the preceding ones, is widely distributed at middle altitudes in the mountains of New Guinea, but it ranges somewhat higher than most of the others.

Genus *PLICAGONUM* Darlington

Plicagonum rugifrons Darlington

Darlington 1952, Part II, p. 174.

Additional material. **West N. G.**: 3, Star Rge., Bivak 36, 1220 m, July 29, 1959, and Bivak 39A, 1500 m, July 1, 3, 10, 1959 (Leiden Mus., Neth. N. G. Exp.). **N-E. N. G.**: 2, Edie Ck. (nr. Wau), 2000, 2100 m, Oct. 4–10, 1961, May 31, 1962 (Sedlaceks). **Papua**: 1, Popondetta, 60 m, Sept. 3–4, 1963 (Sedlacek); 1, Mt. Dayman, Maneau Rge., 1550 m, N Slope No. 5, June 30–July 13, 1953 (Geoffrey M. Tate, AMNH).

Plicagonum fulvum Darlington

Darlington 1952, Part II, pp. 174, 175.

Additional material. **West N. G.**: 4, Star Rge., Bivak 40, 2330, 2360 m, July 19, 22, 29, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. This species is, so far as known, confined to **West N. G.**; the types were from the Snow Mts. However, the following species from the Morobe area, N-E. N. G., is apparently a geographic representative.

Plicagonum kaindi n. sp.

Description. With characters of genus; form *c.* as in *P. fulvum* Darlington (Part II, Fig. 3); dark brown, head almost black, margins of prothorax and appendages more rufous; reticulate microsculpture absent on front, slightly transverse on pronotum, *c.* isodiametric (at most slightly transverse) on elytra. *Head* 0.78 and 0.80 width prothorax; front longitudinally wrinkled at sides, scarcely so at middle, irregularly slightly impressed, sparsely punctulate. *Prothorax* *c.* as in *fulvum*; width/length 1.33 and 1.31; base/apex 1.25 and 1.19; lateral margins wide, moderately reflexed, each with usual 2 setae; disc with usual impressions; base and apex strongly margined; baso-lateral impressions formed mainly by angles between base and lateral margins, not distinctly punctate. *Elytra*: width elytra/prothorax 1.60 and 1.73; base margined, margin rounded at humeri; subapical sinuations moderate, apices more or less (obtusely but usually distinctly) angulate opposite ends 3rd intervals; striae moderately impressed, not distinctly punctulate, intervals flat or slightly convex, 3rd with only 1 (the posterior) dorsal puncture; outer intervals not specially modified apically; no 10th intervals. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate but not lobed; 5th segments without obvious accessory setae. *Secondary sexual characters* normal. *Measurements*: length 15.5–17.5 mm; width 5.6–6.3 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Kaindi, 16 km SW of Wau, **N-E. N. G.**, 2300 m, Oct. 5–7, 1962 (Sedlacek), m. v. light trap; 15 paratypes (some in MCZ, Type No. 31825), same locality, 2200, 2300, 2400 m, dates in Jan., June, Oct., 1962–1963 (Sedlacek), most in m. v. light trap; 1 paratype (AMNH), same locality, 2050 m, May 25, 1959 (L. J. Brass); and 2 paratypes labeled Wau (but perhaps actually from

Mt. Kaindi), 2400 m, Jan. 9–12, 1962 (Sedlaceks and others).

Additional material. **N-E. N. G.**: 1, Bulldog Rd., 19–29 km S of Wau, 2200–2500 m, May 28, 1962 (Sedlacek).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Mt. Kaindi.

Notes. This may be a geographic form of *Plicagonum fulvum* Darlington (above) but *kaindi* is larger, darker, with more strongly angulate (but still obtuse) elytral apices, and (if it proves constant) only 1 puncture on the 3rd elytral interval. The single specimen from Bulldog Rd. is still slightly larger and has virtually simple elytral apices. More material is necessary to show whether it is a distinguishable form.

Genus *LITHAGONUM* Darlington

Lithagonum annulicorne (Maindron)

Darlington 1952, Part II, p. 176.

Additional material: 546, from all three political divisions of New Guinea, and including the following. **Papua**: 485, Peria Ck., Kwagira R., 50 m, "No. 7," Aug. 14–Sept. 6, 1953 (Geoffrey M. Tate, AMNH), evidently taken in light traps; these specimens referable to subspecies *dilutior* Darlington. **N-E. N. G.**: 3, Wau, 1090, 1100 m, Jan. 25, 1963, Sept. 2, 1961 (Sedlaceks); these specimens referable to subspecies *politior* Darlington.

Genus *IRIDAGONUM* Darlington

Darlington 1952, Part II, p. 181.

Generic distribution (revised). Primarily **New Guinea**; represented also on **New Britain** by 1 or more undescribed forms.

Notes. Additional material increases the number of known species of this New Guinean genus from 4 to 7. *I. fessum* is less strongly iridescent above and less strongly punctate below than the other members of the genus, and thus forms a link with *Altagonum*, from which *Iridagonum* may be derived.

The 7 species now known may be distinguished by the following revised key.

Key (Revised) to the Species of *Iridagonum* of New Guinea

1. Third interval of elytron 2-punctate (anterior puncture missing) 2
– Third interval 3-punctate 4
2. Larger (usually over 10 mm; for specimens between 9.3 and 10 mm cf. descriptions); elytral intervals 7 and 8 deeply longitudinally impressed toward apex .... *quadripunctum*
– Smaller (usually under 10 mm); intervals 7 and 8 less impressed 3
3. More slender (width/length prothorax *c.* 1.32); black, strongly iridescent above; in part strongly punctate below .... *quadripunctellum*
– Broader (width/length prothorax *c.* 1.40); often browner and weakly iridescent above (but variable); more weakly punctate below .... *fessum*
4. Two setae over each eye 5
– One seta over each eye (anterior setae missing) 6
5. Eyes normal .... *sexpunctum*
– Eyes smaller, abruptly prominent .... *vigil*
6. Form normal; eyes normal .... *septimum*
– Form fusiform; eyes small, abruptly prominent .... *subfusum*

Iridagonum quadripunctum Darlington

Darlington 1952, Part II, p. 182.

Additional material. Twenty-seven, from all 3 political divisions of New Guinea, and including the following. **N-E. N. G.**: 11, Wau, 1200 m, dates in Jan., Apr., Oct., Nov., Dec. 1961–1963 (Sedlaceks), some in light traps. **West N. G.**: 2, Star Rge., Sibil, 1260 m, June 4, 16, 1959 (Leiden Mus., Neth. N. G. Exp.).

Iridagonum fessum n. sp.

Description. Characters of genus; iridescence weaker and punctation below weaker than usual; form as in Figure 36, very *Agonum*-like; brownish black, appendages not much paler; reticulate microsculpture of head and pronotum more distinct than usual, transverse meshes being visible even on pronotum at 80× magnification; *head* 0.71 and 0.72 width prothorax; eyes normal, 2 setae over each eye. *Prothorax* wide; width/length 1.38 and 1.40; base/apex 1.16 and 1.21; margins rather broadly weakly reflexed, running into shallow subpunctate

baso-lateral impressions. *Elytra* subquadrate; width elytra/prothorax 1.61 and 1.59; sutural angles with small but distinct denticles; 3rd intervals 2-punctate (anterior puncture lacking); 7th and 8th intervals usually slightly impressed toward apex (variable). *Lower surface*: sides of sterna in part subpunctate, abdomen not punctate. *Secondary sexual characters* normal. *Measurements*: length 7.5–8.8 mm; width 3.1–3.9 mm.

Types. Holotype ♂ (Bishop Mus.) and 18 paratypes (some in MCZ, Type No. 31826) all from Wau, **N-E. N. G.**, 1200, 1700–1800 (1 only) m, dates in Jan., Feb., July, Sept., Nov., Dec. 1961–1964 (holotype, 1200 m, Nov. 6–7, 1961) (Sedlaceks), some in m. v. light trap.

Additional material. **N-E. N. G.**: 1, Bulolo, 885 m, Aug. 17, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Sum Sum, 64 km N of Wau, 580 m, Feb. 15, 1963 (W. W. Clissold, Bishop Mus.). **West N. G.**: 1, Sentani, SW Cyclops (Mts.), 100 m, June 15, 1959 (Gressitt); 1, Hol Maffen, 22 km E of Sarmi, July 18, 1959 (T. C. Maa, Bishop Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This is the most *Agonum*-like species of *Iridagonum*. Its recognition characters are given in the preceding revised *Key*.

Iridagonum quadripunctellum Darlington

Darlington 1952, Part II, p. 183.

Additional material. **West N. G.**: 1, Waris, S of Hollandia, 450–500 m, Aug. 8–15, 1959 (T. C. Maa, Bishop Mus.); 1, Hol Maffen, 22 km E of Sarmi, July 18–19, 1959 (T. C. Maa, Bishop Mus.), m. v. light trap.

Notes. Previously known only from the types from Aitape, **N-E. N. G.**

Iridagonum sexpunctum Darlington

Darlington 1952, Part II, p. 184.

Additional material. Seventy, from localities widely scattered in all 3 political divisions of New Guinea, at moderate altitudes, including 19, Wau, 1200, 1250, 2400 (1 specimen only) m, dates in every month *except* Apr., June, 1961–1965 (Sedlaceks and others), some in light trap, m. v. light trap, Malaise trap.

Iridagonum vigil n. sp.

Description. With characters of genus; form as in Figure 37, slightly more convex than usual; dark, strongly iridescent above (as usual). *Head* 0.70 width prothorax; eyes small but abruptly prominent; 2 strong setae over each eye. *Prothorax*: width/length 1.18; base/apex 1.30; lateral margins rather narrow, wider basally, running into poorly defined, finely punctate baso-lateral impressions; disc more convex than usual in genus. *Elytra* subquadrate (not subfusiform); width elytra/prothorax 1.55; sutural angles scarcely (vaguely) denticulate; 3rd interval 3-punctate; outer intervals (7, 8) slightly impressed toward apex. *Lower surface* extensively punctate. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c.* 12 mm; width 4.8 mm.

Type. Holotype ♂ (Leiden Mus.) from Arabu Camp, Wissel Lakes, **West N. G.**, 1800 m, 1939 (H. Boschma); the type is unique.

Notes. See preceding revised *Key* for differential characters of this distinct species.

Iridagonum septimum n. sp.

Description. With characters of genus; form as in Figure 38, slightly more convex than usual; dark, strongly iridescent above on elytra. *Head* 0.64 and 0.65 width prothorax; eyes of moderate size, not unusually prominent, 1 seta over each eye (anterior seta missing). *Prothorax*: width/length 1.12 and 1.12; base/apex 1.25 and 1.30; margins moderate, running into rather long, slightly or vaguely punctate baso-lateral impressions. *Elytra* subquadrate (not subfusiform); width elytra/prothorax 1.53 and 1.56; apices minutely or scarcely subdentic-

ulate; striae more deeply impressed than usual in genus; 3rd interval 3-punctate; intervals 7, 8 weakly (scarcely) impressed at apex. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c.* 12 mm; width 4.8 mm.

Types. Holotype ♂ (Bishop Mus.) from Edie Ck., 14 km SW of Wau, **N-E. N. G.**, 2000 m, Feb. 13, 1962 (Sedlacek); 1 ♂ paratype (MCZ, Type No. 31828) from Goilala, Bome, Owen Stanley Rge., **Papua**, 1950 m, Mar. 8–15, 1958 (W. W. Brandt).

Notes. This is another distinct species adequately characterized in the preceding *Key*. Although the 2 specimens are from different localities, they agree well in form and significant details.

Iridagonum subfusum Darlington

Darlington 1952, Part II, p. 185.

Notes. The holotype, from Ibele Camp, Snow Mts., **West N. G.**, 2550 m, is still the only specimen of this distinct species known.

Genus *ALTAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 185.

Diagnosis (*revised*). Size small or medium (not over 14.5 mm); wing-and-seta formula + w, (+)+, –(+), (+)(+)(+) (see Part II, p. 107, for explanation); other characters in general as in *Notagonum*, but details more variable.

Notes. This "genus of convenience" includes a number of New Guinean species, not necessarily all related, but sharing at least the diagnostic characters stated above. Most species of this genus are mountain-living, although a few occur at or descend to sea level. This is in contrast to the species of *Notagonum*, most of which occur at low altitudes, although some of these too are mountain-living. Twenty-four species and 4 additional subspecies from New Guinea were assigned to *Altagonum* in 1952. Ten additional species are described now, and several more that may be new are represented in the material before me by single specimens that I prefer not to describe now.

In the following pages all species found in the Morobe area, but not previously recorded from there, are noted, as are other important records of previously described species.

Iridagonum fessum (described above) might be mistaken for an *Altagonum*, since the dorsal iridescence and the punctation of the lower surface are less obvious than usual in *Iridagonum*. In my key to the New Guinean species of *Altagonum* (Part II, pp. 188ff), *fessum* would run to couplet 8 but differs from the species there named (*nox* Darlington, etc.) in being usually browner (less black), with sutural angles of elytra conspicuously denticulate, and baso-lateral area of pronotum as well as sides of sterna plainly punctate in clean specimens.

The 10 new species of *Altagonum* that I am now describing all have (in addition to the generic characters) one or more of the following special characters: *either* posterior-lateral (as well as the median-lateral) prothoracic setae lacking, *or* less than 3 (either 2 or 0) punctures on each 3rd elytral interval, *or* elytra spined. I therefore offer the following key to all known New Guinean species of *Altagonum* that have one or more of these characters. This new key supplements but of course does not entirely supersede the *Key to the Species of Altagonum of New Guinea* in Part II, pp. 188–189.

Supplementary Key to Certain New Guinean *Altagonum*

1. Posterior-lateral pronotal setae present, *and* 3rd intervals of elytra 3-punctate, *and* elytra spined 2
– Posterior-lateral pronotal setae absent *or* 3rd intervals with only 2 setae or none (elytra spined or not spined) 6
2. Elytral spines *c.* opposite ends of sutural intervals 3
– Elytral spines *c.* opposite ends of 3rd intervals 4
3. Length *c.* 8 mm .... *tutum*
– Length *c.* 11 mm .... *cracens*
4. Black, iridescent; length *c.* 14.5 mm .... *avium*
– Elytra greenish or bluish; length *c.* 11–13 mm 5

5. Prothoracic margins narrow anteriorly, wide posteriorly .... *cheesmani*
– Prothoracic margins wide anteriorly as well as posteriorly .... *sororium*
6. Posterior-lateral prothoracic setae present 7
– Posterior-lateral prothoracic setae absent 13
7. Third intervals of elytra 2-punctate 8
– Third intervals of elytra impunctate (form of *grossulum*, etc.) .... *exutum*
8. Elytra not spined 9
– Elytra spined 11
9. Subfusiform; prothoracic base/apex *c.* 1.70 or more .... *parascapha*
– *Agonum*-like; prothoracic base/apex *c.* 1.50 or less 10
10. Black; length 6.8–9.7; elytral apices angulate .... *vallicola*
– Brown; length 5.3–7.5 mm; elytral apices not angulate .... *grossulum* .... (and) *grossuloides*
11. Length *c.* 8 mm or less (brownish black) .... *scapha*
– Larger 12
12. Length *c.* 9 mm (elytra submetallic) .... *regiscapha*
– Length *c.* 11 mm (brown) .... *erugatum*
13. Two pairs supraocular setae present 14
Anterior pair supraocular setae absent 17
14. Elytra spined .... *stellaris*
– Elytra not spined 15
15. Form broad *Calathus*-like; prothorax width/length *c.* 1.30 or more .... *nudicolle*
– More slender 16
16. Length *c.* 10 mm .... *fatuum*
– Length *c.* 8 mm .... *tenellum*
17. Form broad *Calathus*-like; prothorax width/length *c.* 1.45 .... *bigenum*
– Similar but prothorax more wedge-shaped; prothoracic width/length *c.* 1.60 .... *subconicolle*

Altagonum vallicola Darlington

Darlington 1952, Part II, pp. 188, 190.

Additional material. **N-E. N. G.**: 1, Bulolo, Morobe Dist. 1000 m, Aug. 17, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Wareo, Finschhafen (Rev. L. Wagner, South Australian Mus.); 1, Adelbert Mts.: Wanuma, 800–1000 m, Oct. 27, 1958 (Gressitt), light trap. **West N. G.**: 3, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman); 1, Waigeo Is., Mt. Nok, Camp 2 (Buffelhorn), June 1938 (Cheesman).

Notes. Except for the specimens from Japen Island (which are virtual topotypes of subspecies *subvividum* Darlington), I have not attempted to assign the *Additional specimens* to subspecies.

The specimen from Mt. Nok, Waigeo Is., is noteworthy. Externally, except for the absence of anterior-lateral pronotal and anterior dorsal elytral punctures, it is virtually indistinguishable from 5 specimens of *Notagonum addendum* (above) also from Mt. Nok, but from a different locality on the mountain. The similarity extends to proportions, exact form of elytral apices, and other usual characters, except for a very slight difference in the 4th hind-tarsal segment, of which the outer angle is slightly longer than the inner in *Notagonum addendum*, but equal to the inner in *Altagonum vallicola*. The whole similarity is so great that I was prepared to consider these two insects dimorphic forms of one species, until I dissected the male copulatory organs. These are strikingly different, more slender and more arcuate in *N. addendum*, much stouter and less arcuate in *A. vallicola*. Further study, with more material, will be necessary to decide the real relationship (if any) between these two species.

Altagonum grossulum Darlington (and) *Altagonum grossuloides* Darlington

Darlington 1952, Part II, pp. 188, 191, 194.

Additional material. Ninety-one, from all three political divisions of New Guinea, at altitudes from near sea level to 2770 m (Mt. Wilhelm), but *not* yet found in the vicinity of Wau.

Notes. This material forms a confusing taxonomic complex in which variation is notable not only in form (*e. g.*, in relative width/length of prothorax), elytral microsculpture, and size, but also in punctures of third elytral intervals, in depth of elytral striae, and in color. The third intervals are each 2-punctate in most individuals (anterior puncture lacking) as originally described, but 7 specimens from the Wissel Lakes area, West N. G., have the third intervals 3-punctate on both elytra, although

these specimens seem referable to *grossulum* or *grossuloides* otherwise. In color, individuals vary from uniformly dark (except lateral margins of prothorax and elytra rather narrowly yellowish-translucent) to elytra mainly pale brown with subapical dark areas on intervals 2–6 (longest on latter), the dark areas together setting off a squarish apical pale spot that recalls the apical spot of *Trichotichnus* (*Lampetes*) *guttula* Darlington (1968, Part III, p. 57). The entire color variation occurs in a series from Saidor, Finisterre Range (Bishop Mus.) and in another series from other localities on the Finisterre Rge. (Bacchus, British Mus.). These series give the impression that the color may be partly genetically dimorphic, Mendelian. Analysis of the variation in this new material requires third-stage taxonomic treatment, and is more than I can undertake now. The material is mainly in the Bishop Museum, British Museum, Leiden Museum, AMNH, CSIRO, and South Australian Museum. The following new species, although without punctures on the third elytral intervals, seems otherwise closely related to *grossulum* and *grossuloides* and should be considered in future studies of this group of *Altagonum*.

Altagonum exutum n. sp.

Description. With characters of genus. Form of *A. grossuloides* (*c.* of small *Agonum s. s.*); brownish black, appendages yellowish brown, lateral margins of prothorax and elytra yellowish-translucent; reticulate microsculpture isodiametric on front, transverse on pronotum, strongly transverse on elytra; latter faintly iridescent in proper light. *Head* 0.66 and 0.65 width prothorax. *Prothorax* rather large; width length 1.38 and 1.39; base apex 1.55 and 1.50; sides moderately arcuate, moderately converging and sometimes slightly sinuate before obtuse but *c.* well-defined posterior angles; disc and impressions as in other members of group, virtually impunctate. *Elytra*: width elytra prothorax 1.46 and 1.50; not or not much impressed before middle; humeral margins angulate, blunted; apices normal, *c.* simple; striae well impressed, impunctate; intervals usually convex, 3rd without dorsal punctures. *Lower surface*: virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment simply emarginate. *Measurements*: length 6.0–7.2 mm; width 2.5–2.9 mm.

Types. Holotype ♂ (Bishop Mus.) and 1 ♀ paratype (MCZ, Type No. 31829) from Wau, Morobe Dist., **N-E. N. G.**, 1250 m, Feb. 14 (holotype) and Jan. 11, 1963 (Sedlacek), and additional paratypes as follows. **N-E. N. G.**: 1, Finschhafen (Wagner, South Australian Mus.), "trapped by sticky seeds of *Pisonia brunoniana*"; 1, Herzog Rge., Vagau, *c.* 4000 ft. (1220 m), Jan. 4–17, 1965 (Bacchus, British Mus.); 2, "No. 10," Purosa Camp, Okapa area, 1950 m, Sept. 23, 24, 1959 (L. J. Brass, Sixth Archbold Exp., AMNH). **Papua**: 3, Mt. Dayman, Maneau Rge., N Slope "No. 5," June 30–July 13, 1953 (Geoffrey M. Tate, AMNH); 1, Doveta, and 1, Komania, Amazon Bay Dist., Aug. and Nov., 1962 (W. W. Brandt, CSIRO).

Measured specimens. The ♂ holotype and ♀ paratype from Wau.

Notes. In form and most characters this species resembles *grossulum* Darlington and *grossuloides* Darlington, but it differs from these species in lacking dorsal punctures on the 3rd elytral intervals. See also preceding *Supplementary Key*.

Altagonum nox Darlington

Darlington 1952, Part II, pp. 188, 194.

Additional material. **West N. G.**: 1, Star Rge., Bivak 39A, 1500 m, July 9, 1959 (Leiden Mus., Neth. N. G. Exp.).

Altagonum magnox Darlington

Darlington 1952, Part II, pp. 188, 195.

Additional material. **West N. G.**: 2, Star Rge., Sibil and Bivak 39A, 1260, 1500 m, June and July 10, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. Specimens seen of possibly related

forms are: 1, Bivak 40, 2330 m, Star Rge., **West N. G.** (Leiden Mus.); 1, Saidor, Finisterre Rge., **N-E. N. G.** (Bishop Mus.); 2, Mt. Dayman, Maneau Rge., **Papua** (AMNH).

Altagonum japenox Darlington

Darlington 1952, Part II, pp. 189, 196.

Additional material: 1 crushed ♀, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Altagonum pubinox Darlington

Darlington 1952, Part II, pp. 189, 196.

Additional material. **N-E. N. G.**: 2, Mt. Kaindi, 16 km SW of Wau, 2300 m, Oct. 6, 5–7, 1962 (Sedlacek), light trap.

Altagonum noctellum Darlington

Darlington 1952, Part II, pp. 189, 197.

Additional material. **N-E. N. G.**: 2, Waigeu Is., Camp Nok, 2500 ft. (*c.* 660 m), Apr. 1938 (Cheesman); 1, Wau, 1450 m, Feb. 6, 1963 (Sedlacek); 1, Mt. Kaindi (near Wau), 2350 m, Jan. 10, 1962 (Sedlaceks); 1, Lae, July 1944 (F. E. Skinner, Purdue U. Coll.); 1, Eliptamin Vy., 1200–1350 m, June 19–30, 1959 (W. W. Brandt, Bishop Mus.); 1, 22 km SE Okapa, 2100 m, Aug. 28, 1964 (Sedlaceks). **Papua**: 2, Popondetta, 25 m, May, June 1966 (Shanahan-Lippert, Bishop Mus.), light trap; 2, Goodenough Is., E Slope No. 10, 900 m, Oct. 24–30, 1953 (Geoffrey M. Tate, AMNH).

Altagonum planinox Darlington

Darlington 1952, Part II, pp. 189, 198.

Additional material. **N-E. N. G.**: 1, Wau, 1250 m, Jan. 5, 1963 (Sedlacek), m. v. light trap. **Papua**: 1, Goodenough Is., E Slope No. 10, 900 m, Oct. 24–30, 1953 (Geoffrey M. Tate, AMNH); 2, Fergusson Is., Mts. between Agamoia and Ailuluai, 900 m, "No. 4," June 5–17, 1956 (Fifth Archbold Exp., L. J. Brass, AMNH).

Altagonum dilutipes Darlington

Darlington 1952, Part II, pp. 189, 198.

Additional material. **N-E. N. G.**: 4, Wau, 1200 m, dates in Sept., Nov., Dec., 1961–1965 (Sedlaceks & others), some in m. v. light trap; 1, Karimui, S of Goroka, 1000 m, June 8, 1961 (Gressitts). **West N. G.**: 4, Swart Vy., Karubaka, 1450 m, Nov. 10, 12, 1958 (Gressitt), light trap; 8, Star Rge., Sibil and Bivak 39A, 1260, 1500 m, dates in May, June, July, 1959 (Leiden Mus., Neth. N. G. Exp.), some at light.

Notes. Some of the specimens listed above, especially those from the Star Range, are intermediate between *dilutipes* and *europhilum* Darlington. Only third-stage taxonomic study can decide the status of these two species.

Altagonum europhilum Darlington

Darlington 1952, Part II, pp. 189, 199.

Additional material. **N-E. N. G.**: 1, Mt. Piora, (Kratke Rge.), 2100 m, June 12, 1966 (Gressitts), Malaise trap.

Notes. The types were from the Snow Mts., **West N. G.** The single specimen recorded above is definitely *europhilum* rather than *dilutipes*, with prothoracic length width only *c.* 1.20.

Altagonum pallinox Darlington

Darlington 1952, Part II, pp. 189, 200.

Additional material. **N-E. N. G.**: 3, Wau, 1200, 1700 m, dates in Feb., June, Sept., 1961, 1963 (Sedlaceks), 2 of these in light trap; 3, Eliptamin Vy., 1200–1350, 1665–2530 m, June 19–30, Aug. 16–30, 1959 (W. W. Brandt, Bishop Mus.).

Altagonum caducum Darlington

Darlington 1952, Part II, pp. 189, 202.

Additional material. One hundred thirty-three, from all 3 political divisions of New Guinea, altitudes from 1200–2770 m, material mainly in Bishop Mus., British Mus.,

Leiden Mus., AMNH. Included are: 23, Wau and Edie Ck., 1200 to 2400 m, Jan., Feb., May, Oct., 1961–1963 (Sedlaceks), some in light trap.

Notes. This material would probably repay third-stage taxonomic study.

Altagonum sphodrum Darlington

Darlington 1952, Part II, pp. 189, 204.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 2800–2900 m, July 6, 1963 (Sedlacek); 2, Laiagam, 2520 m, June 24, 1963 (Sedlacek). **Papua**: 1, Mt. Giluwe, 2500 m, May 1, 1963 (Sedlacek).

Notes. This distinct species appears to be restricted to relatively high altitudes on and near (west and south of) the Bismarck Rge.

Altagonum postsulcatum Darlington

Darlington 1952, Part II, pp. 189, 205.

Additional material. Thirty-four, from localities in **N-E. N. G.** and **West N. G.**, 1200 to 2550 m. Included are: 13, Wau and Edie Ck., 1200 to 2350 m, Oct., Nov., 1963 (Sedlaceks), some in light trap.

Notes. This is another species that would probably repay third-stage taxonomic study, especially comparison of series now available from the Morobe area (Wau etc.) and the Snow Mts.

Altagonum misim Darlington

Darlington 1952, Part II, pp. 189, 206.

Additional material. One hundred, from all three political divisions of New Guinea, at altitudes from 900 ft. (275 m) to 2400 m. Included are the following. **N-E. N. G.**: 1, Wau, 2400 m, Jan. 9–12, 1962 (Sedlaceks and others); 1, Edie Ck. nr. Wau, 2000 m, Oct. 4–10, 1961 (Sedlaceks), light trap; (the types were from Mt. Mis(s)im, near Wau, 6400 ft. (1950 m)); 65, Great Cave, Telefomin, 4700 ft. (1435 m), (Victor Emmanuel Rge.), various dates (B. Craig, T. Hayllar). **West N. G.**: 7, Star Rge., Sibil Vy., 1245 m, Oct. 18–Nov. 8, 1961 (L. W. Quate, Bishop Mus.); 2, Star Rge., Bivak 36, Bivak 39A, 1220, 1500 m, July 10, 29, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. This species too would repay third-stage taxonomic study. The population on the Star Range is probably distinguishable, characterized by reduced elytral denticles. The ecology of the individuals from Great Cave, Telefomin, will probably be reported on by Mr. Elery Hamilton-Smith, of the South Australian Museum.

Altogonum cheesmani Darlington

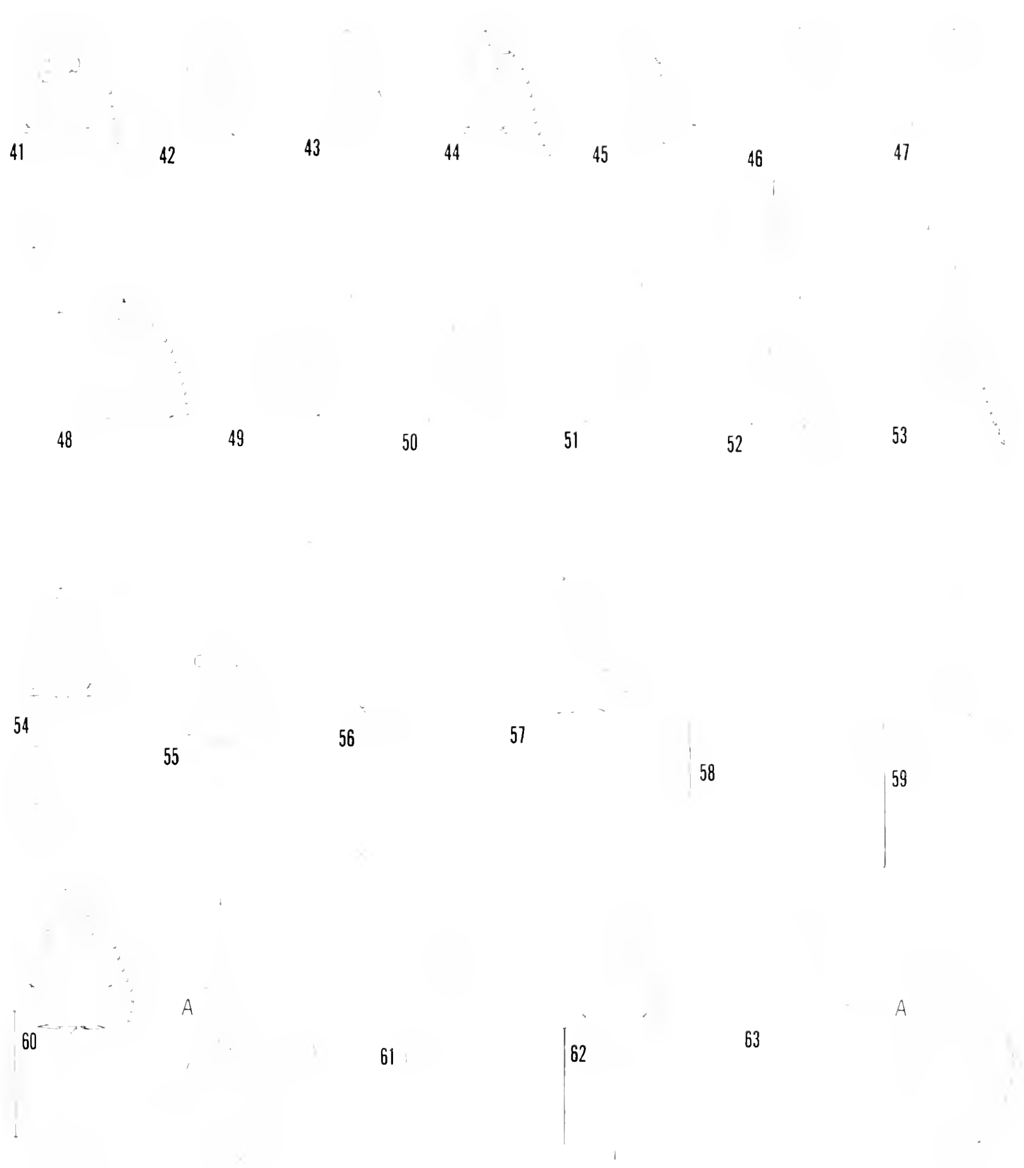
Darlington 1952, Part II, pp. 189, 207.

Additional material. **N-E. N. G.**: 5, Wau, 1200–1450 m, Feb., Apr., May, Oct., Nov., 1962, 1963 (Sedlaceks, Shanahan), m. v. light trap, Malaise trap; 1, Mt. Hagen, W Highlands, Oct. 1961 (W. W. Brandt, CSIRO).

Notes. The unique type of this species is from Mafulu, **Papua**, 4000 ft. (1220 m). The color of this species is variable, the elytra of the type being green but of the additional specimens now recorded purple or purplish. The form is as in Figure 39.

Altagonum sororium n. sp.

Description. With characters of genus; form as in Figure 40, rather slender, convex, with large eyes and short-spined elytra; head and disc of pronotum black or red, the pronotum with wide testaceous-translucent margins, elytra bluish or purplish, appendages reddish or brownish testaceous; shining, reticulate microsculpture absent on front and pronotal disc, strongly transverse on elytra. *Head* 0.81 and 0.82 width prothorax. *Prothorax*: width/length 1.30 and 1.35; base/apex 1.73 and 1.63; sides variably sinuate just before blunted or narrowly rounded basal angles; lateral margins wide and widely reflexed anteriorly as well as posteriorly, each with seta-bearing puncture on margin at basal angle; apex slightly emarginate; base and apex margined; disc with transverse impressions deep, middle



Figures **41—63A** (see text, section [15]): **41**, *A. parascapha* n. sp., ♂ holotype; **42**, *A. tenuellum* n. sp., ♂ holo.; **43**, *A. stellaris* n. sp., ♂ holo.; **44**, *A. cracens* n. sp., ♂ holo.; **45**, *A. avium* n. sp., ♀ holo.; **46**, *A. erugatum* n. sp., ♀ holo.; **47**, *A. bigenum* n. sp., ♂ holo.; **48**, *A. subconicolle* n. sp., ♂ holo.; **49**, *Maculagonum seripox* n. sp., ♀ paratype, Wau; **50**, *M. daymanpax* n. sp., ♂ holo.; **51**, *M. canipax* n. sp.; ♂ holo.; **52**, *M. atropox* n. sp., ♂ holo.; **53**, *M. depilapox* n. sp., ♀ para., Mt. Giluwe; **54**, *M. waupox* n. sp., ♂ para., Mt. Koindi; **55**, *M. kaindipox* n. sp., ♂ holo.; **56**, *Potamagonum postsetosum* n. sp., ♂ holo.; **57**, *Idiagonum limatulum* n. sp., ♂ holo.; **58**, *Montagonum anax* n. sp., ♂ holo.; **59**, *M. anassa* n. sp., ♀ holo.; **60** *M. nepos* n. sp., ♀ para.; **60A**, same, copulatory organs, holo.; **61**, *M. sararcula* n. sp., ♀ holo.; **62**, *M. pandum* n. sp., ♂ holo.; **63** *M. fugitum* n. sp., ♂ holo.; **63A**, same, copulatory organs, same individual.

line rather fine, surface not or not much punctate even in baso-lateral impressions. *Elytra* long; width elytra/prothorax 1.42 and 1.47; apices each with short acute spine in line of 3rd interval; striae impressed, punctate; 3rd interval 3-punctate, outer intervals not impressed apically. *Lower surface* punctate only at sides of mesosternum; abdomen not pubescent. *Legs*: 4th hind-tarsal segment rather deeply emarginate but not strongly lobed, outer angle slightly more prominent than inner. *Measurements*: length 10.8–12.0 mm; width 3.6–4.0 mm.

Types. Holotype ♂ (Bishop Mus.) and 2 (♂♂) paratypes (1 in MCZ, Type No. 31830) from Waris, S of Hollandia, **West N. G.**, 450–500 m, Aug. 1–2, 1959 (T. C. Maa), and additional paratypes as follows. **N-E. N. G.**: 1, Pindiu, Huon Pen., Apr. 20, 1963 (Sedlacek); 1, Korop, Upper Jimmi Vy., 1300 m, July 12, 1955 (Gressitt); 1, Tsenga, Upper Jimmi Vy., 1200 m, July 15, 1955 (Gressitt).

Additional material. **Papua**: 1, Kokoda-Pitoki, 400 m, Mar. 23, 1956 (Gressitt).

Measured specimens. The ♂ holotype and the ♀ paratype from Korop.

Notes. Although probably related to *A. cheesmani*, the present new species differs in having the prothoracic margins wide anteriorly as well as posteriorly (the margins are relatively very narrow anteriorly in *cheesmani*). See also preceding *Supplementary Key*. The present, limited material suggests that *cheesmani* usually occurs at somewhat higher altitudes (above 1000 m) while *sororium* descends to lower altitudes, although the ranges of the two overlap.

Altagonum scapha Darlington

Darlington 1952, Part II, pp. 189, 208.

Additional material: 12, from all 3 political divisions of New Guinea (but none from Morobe area), altitudes given from "100–700" to 1700 m.

Notes. This material shows virtually continuous variation from elytra with short spines to elytra only obtusely angulate at apex. Third-stage taxonomic study is needed to show whether more than one species is involved.

Altagonum parascapha n. sp.

Description. With characters of genus; form as in Figure 41, more parallel (less fusiform) than *scapha*, moderately convex; dark rufous to piceous, appendages reddish; shining, reticulate microsculpture indistinct on front and pronotal disc, strongly transverse on elytra. *Head* 0.66 and 0.67 width prothorax. *Prothorax*: width/length 1.32 and 1.36; base/apex 1.70 and 1.75 (but anterior angles not distinct, so measurement an approximation); sides *c.* evenly rounded, at most straighter or faintly sinuate posteriorly; lateral margins moderate, narrow anteriorly, not strongly reflexed, each with seta-bearing puncture a little in from edge of margin near posterior angle; base and apex finely margined; disc with middle line and transverse impressions moderate, baso-lateral impressions shallow, not or not distinctly punctate. *Elytra*: width elytra/prothorax 1.48 and 1.58; humeral angles *c.* rectangular; subapical sinuations virtually absent; apices usually obtusely angulate opposite 3rd intervals (but angulation variable), with sutural angles usually subdenticulate; striae moderately impressed, not distinctly punctulate; intervals nearly flat, 3rd 2-punctate (anterior puncture absent), outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 5th hind-tarsal segment moderately emarginate, not distinctly lobed. *Measurements*: length 8.3–8.5 mm; width 3.0–3.3 mm.

Types. Holotype ♂ (Bishop Mus.) and 2 paratypes (1 in MCZ, Type No. 31831) from Swart Vy., Karubaka, **N-E. N. G.**, 1550 m, Nov. 8, 1958 (Gressitt); 2 paratypes, Pindiu, Huon Pen., **N-E. N. G.**, 1 labelled 1200–1450 m, Apr. 18, 20, 1963 (Sedlacek).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Karubaka.

Notes. As compared with *A. scapha* Dar-

lington, the present new species is less fusiform, with prothorax relatively slightly wider, slightly more narrowed behind, and with somewhat wider margins, and *parascapha* has obtusely angulate or subangulate elytral apices (apices spined or more distinctly angulate in *scapha*). Direct comparison leaves no doubt that the two species are distinct, and I am not even sure that they are directly related.

Altagonum latilimbus Darlington

Darlington 1952, Part II, pp. 189, 210.

Additional material. **N-E. N. G.**: 7, Wau, 2400 m (none lower), Jan. 1962 (Sedlaceks etc.); 8, Mt. Kaindi, 16 km SW of Wau, 2200, 2300, 2350 m, June, Oct., 1962 (Sedlaceks), some in m. v. light trap; 1, Main Finisterre Rge. nr. Freyberg Pass (N), 2550 m, Oct. 1–21, 1958 (W. W. Brandt, Bishop Mus.). **Papua**: 1, Owen Stanley Rge., Goilala, Tororo, 1560 m, Feb. 15–20, 1958 (W. W. Brandt, Bishop Mus.).

Notes. Although *latilimbus* was described from the Snow Mts., **West N. G.**, and although another species (*paralimbus* Darlington) is known from Mt. Mis(s)im in the Morobe area, the specimens recorded above are all *latilimbus*, all being relatively wide and having the dark discal color of the elytra not extended along the suture toward apex.

Altagonum nudicolle Darlington

Darlington 1952, Part II, pp. 189, 211.

Additional material. **N-E. N. G.**: 2, Daulo Pass (Asaro-Chimbu Div.), 2800 m, June 14, 1955 (Gressitt); 1, Mt. Elandora, Oct. 15, 1965 (Dept. Agr. Port Moresby). **Papua**: 1, Mt. Giluwe, N side, Malgi, 2500 m, May 25–30, 1961 (Gressitt).

Notes. This species (which, like all *Altagonum*, is winged) is evidently widely distributed in the higher mountains (above 2000 m) of N-E. N. G. (south of the Ramu-Markham Valley) and the NW corner of Papua. The long series (the types) that I collected on Mt. Wilhelm were under cover on the ground in wet mountain forest.

Altagonum tenuellum n. sp.

Description. With characters of genus; form as in Figure 42, small, slender; brown, appendages slightly paler; reticulate microsculpture *c.* isodiametric on front, transverse on pronotum and elytra, in part indistinct or imperfect on latter. *Head* 0.74 and 0.71 width prothorax. *Prothorax*: width/length 1.11 and 1.08; base/apex 1.51 and 1.53; sides weakly arcuate, sinuate near *c.* right slightly blunted basal angles; lateral margins rather narrow, weakly reflexed, somewhat wider and more reflexed toward base, without setae; disc normally impressed, baso-lateral impressions weak, surface slightly irregular but not punctate. *Elytra*: width elytra/prothorax 1.72 and 1.81; margins *c.* right (slightly obtuse) at humeri; subapical sinuations slight, apices slightly irregularly rounded, sutural angles not distinctly denticulate; striae impressed, not punctulate; intervals slightly convex, 3rd without dorsal punctures, outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment weakly emarginate, not lobed. *Measurements*: length *c.* 8 mm; width 2.9–3.1 mm.

Types. Holotype ♂ (MCZ, Type No. 31832) from Mt. Maneo, vic. Milne Bay, **Papua**, "8–10–1961" (John Latter), at light; and 1 ♀ paratype (AMNH), Mt. Dayman, Maneau Rge., **Papua**, 1550 m, N Slope No. 5, June 30–July 13, 1953 (Geoffrey M. Tate).

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters of this species.

Altagonum stellaris n. sp.

Description. With characters of genus; form as in Figure 43, large, slender, with long appendages; black, margins of prothorax slightly reddish, femora dark, tibiae, tarsi, and antennae reddish brown; reticulate microsculpture light and *c.* isodiametric on

front, light and transverse on pronotum, more distinct and strongly transverse on elytra. *Head* 0.81 width prothorax. *Prothorax*: width/length 1.01; base/apex 1.22; lateral margins rather wide, scarcely narrower anteriorly than posteriorly; rather strongly reflexed especially posteriorly, without seta-bearing punctures; base and apex finely margined; disc rather strongly convex, impressed as usual, with poorly defined baso-lateral impressions slightly irregular but not distinctly punctate. *Elytra*: width elytra/prothorax 1.55; margins obtusely angulate at humeri; apices each with moderate spine *c.* in line of 3rd interval; striae impressed, not punctulate; intervals slightly convex, 3rd 3-punctate (but middle puncture lacking on left elytron, and 2nd and 3rd striae pulled together and connected by impressions at anterior and posterior punctures); outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: hind tarsi missing. *Measurements*: length 14.8 mm; width 4.3 mm.

Type. Holotype ♂ (Leiden Mus.) from Star Rge., **West N. G.**, Bivak 39A, 1500 m, July 9, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters.

Altagonum cracens n. sp.

Description. With characters of genus; form as in Figure 44, moderately large, slender, with long appendages; brownish black, femora and outer sides of tibiae scarcely paler, tarsi and antennae more brownish; reticulate microsculpture light and *c.* isodiametric on front, more distinct and transverse on pronotum and elytra. *Head* 0.90 width prothorax. *Prothorax*: width/length 0.99; base/apex 1.34; lateral margins moderate, slightly broader posteriorly, moderately reflexed, each with seta-bearing puncture on edge of margin at base; base and apex finely margined; disc normally convex, with usual impressions, baso-lateral impressions moderate, poorly defined, not punctate. *Elytra*: width elytra/prothorax 1.96; margins at humeri very obtuse; apices each with short spine near suture, with sutural interval running onto spine, but spines slightly dehiscent; striae impressed, not punctulate; intervals slightly convex, 3rd 3-punctate, outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment moderately emarginate at apex. *Measurements*: length 11.0 mm; width 3.6 mm.

Type. Holotype ♂ (South Australian Mus.) from Great Cave, Telefomin, (Victor Emmanuel Rge.), **N-E. N. G.**, (4700 ft. = 1435 m) May 31, 1965 (T. Hayllar); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters.

Altagonum avium n. sp.

Description. With characters of genus; form as in Figure 45, large, subparallel, normally convex; black, femora and tibiae dark, tarsi and antennae browner; shining, elytra and (less so) pronotum moderately iridescent, reticulate microsculpture *c.* isodiametric on front, imperfect (probably fine and strongly transverse) on pronotum and elytra. *Head* 0.67 width prothorax. *Prothorax*: width/length 1.15; base/apex *c.* 1.00 (posterior angles too rounded to measure accurately); lateral margins arcuate for entire length to broadly rounded posterior angles, moderately wide, slightly wider posteriorly, rather strongly reflexed, each with seta on inner face (not edge) of margin well before base; base and apex finely margined; disc with middle line light but *c.* entire, posterior transverse impression well marked, anterior impression scarcely indicated, deep baso-lateral impressions formed by union of posterior transverse impression with basal-marginal channels, impunctate. *Elytra*: width elytra/prothorax 1.30; margins at humeri *c.* right (slightly obtuse, slightly blunted); apices each with short spine in line of 3rd interval; striae impressed, not punctulate; intervals slightly

convex, 3rd 3-punctate; outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment deeply emarginate, lobed, with outer lobe longer than inner. *Measurements*: length 14.5 mm; width 5.5 mm.

Type. Holotype ♀ (MCZ, Type No. 31835) from Mt. Elandora (Kratke Rge.), **N-E. N. G.**, Oct. 17, 1965 (collector not given); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters. This species may actually be related to (ancestral to?) certain *Fortagonum* but has fully developed inner wings and two strong seta-bearing punctures over each eye.

Altagonum erugatum n. sp.

Description. With characters of genus; form as in Figure 46, *Calathus*-like, subfusiform, rather strongly convex; dark brown, appendages somewhat paler; reticulate microsculpture *c*. isodiametric on front, transverse on pronotum and elytra. *Head* 0.66 width prothorax. *Prothorax*: width/length 1.00; base/apex *c*. 1.58 (anterior angles not distinct); sides weakly arcuate, *c*. straight but not sinuate to slightly obtuse, narrowly rounded basal angles; lateral margins very narrow anteriorly, wider and weakly reflexed posteriorly, each with seta-bearing puncture on inner face (not edge) near base; base and apex finely margined; disc with middle line distinct but light and short, transverse impressions almost obsolete, baso-lateral impressions scarcely impressed, impunctate (slightly roughened). *Elytra*: width elytra/prothorax 1.48; margins acutely angulate at humeri; apices each with short spine (acute tooth) in line of 3rd interval; striae impressed, scarcely punctulate; intervals *c*. flat, 3rd 2-punctate (anterior puncture missing); outer intervals not distinctly impressed apically. *Lower surface* impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate, scarcely lobed. *Measurements*: length 11.0 mm; width 3.9 mm.

Type. Holotype ♀ (Leiden Mus.), from Bivak 39A, Star Rge., **West N. G.**, 1500 m, July 23, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters. However, this species does not seem closely related to any other.

Altagonum bigenum n. sp.

Description. With characters of genus, except anterior supraocular setae lacking; form as in Figure 47, subfusiform (broad *Agonum*-like); black, elytra weakly iridescent or purplish in some lights, appendages dark; reticulate microsculpture very light, isodiametric on front, transverse on pronotal disc, probably more transverse but scarcely distinct on elytra. *Head* 0.51 and 0.54 width prothorax; posterior supraocular setae present, anterior absent; mentum tooth narrow, not emarginate. *Prothorax*: width/length 1.44 and 1.46; base/apex 1.63 and 1.62; lateral margins obsolete anteriorly, broad and slightly explanate posteriorly, without seta-bearing punctures; apex finely margined, base not margined; disc with middle line distinct, transverse impressions very weak, baso-lateral impressions almost obsolete (except for very obtuse depression between margin and disc), irregularly faintly subpunctate. *Elytra*: width elytra/prothorax 1.32 and 1.39; base margined, margins *c*. right or slightly obtuse at humeri; subapical sinuations obsolete or nearly so, apices each with very short spine *c*. in line of 3rd interval; striae lightly impressed, slightly irregular but scarcely punctulate; intervals nearly flat or slightly convex, 3rd 2-punctate (anterior puncture missing), outer intervals not impressed toward apex, no 10th intervals. *Inner wings* fully developed. *Lower surface* virtually impunctate except mesepisterna faintly punctate; abdomen not pubescent. *Legs*: hind tarsi slender, sulcate each side above, with 4th segment rather long, deeply emarginate,

slightly lobed, with outer lobe longer than inner; 5th hind-tarsal segments without accessory setae. *Secondary sexual characters* normal. *Measurements*: length *c.* 10.5–11.5 mm; width 4.3–5.0 mm.

Types. Holotype ♂ (MCZ, Type No. 31837) from Okapa, Purosa, **N-E. N. G.**, Feb. 27, 1965 (Hornabrook), and 5 paratypes as follows, all ♀♀. **N-E. N. G.**: 1, E Highlands, Purosa (same locality as holotype), 1700 m, May 17–25, 1966 (Gressitt & Tawi); 1, Aiyura, 1550 m, May 13, 1966 (Gressitt), light trap; 1, Wau, Morobe Dist., 1200 m, June 25, 1961 (Sedlaceks); 1, Pindiu, Huon Pen., 870–1300 m, Apr. 21–22, 1963 (Sedlacek). **Papua**: 1, Owen Stanley Rge., Goilala: Loloipa, Feb. 1–15, 1958 (W. W. Brandt, Bishop Mus.).

Measured specimens. The ♂ holotype and the ♀ paratype from Wau.

Notes. If it were not fully winged (and the capture of one in a light trap suggests that it really flies), I would refer this species to *Fortagonum* because of the absence of anterior supraocular setae, and in describing it I have noted characters of value in *Fortagonum* but not (as a rule) useful in *Altagonum*. This species may actually be something like the ancestor from which *Fortagonum* has been derived. However, in my (practical rather than phylogenetic) generic classification, it fits best in *Altagonum*, from all other known species of which (except the following) it differs in lacking anterior supraocular setae. In form, it is something like a rather stout *A. erugatum* (described above), but it differs in so many details that I am not sure there is real relationship. The present new species is represented in extreme western New Guinea by the following presumably geographic isolate.

Altagonum subconicolle n. sp.

Description. With characters of genus, except anterior supraocular setae lacking; form as in Figure 48, *c.* as in preceding (*bigenum*) except that prothorax is differently formed, relatively slightly wider, with straighter (but converging) sides and more conspicuous anterior angles. Characters otherwise *c.* as in *bigenum*, including prothoracic margins without seta-bearing punctures and 3rd elytral intervals each 2-punctate. Proportions: width of head/prothorax 0.50; prothoracic width/length 1.61, base/apex 1.58; width elytra/prothorax 1.27. *Measurements*: length *c.* 11.0 mm; width 4.7 mm.

Type. Holotype ♂ (Bishop Mus.) from Fak Fak, S coast of Bomberai, Vogelkop, **West N. G.**, 100–700 m, June 9, 1959 (T. C. Maa); the type is unique.

Notes. Although this is apparently a representative form of *A. bigenum*, I prefer to consider it a species rather than a subspecies until more material showing distribution of both forms is available. The single specimen of the present form was taken at a substantially lower altitude than any of the specimens of *bigenum*.

Genus *MACULAGONUM* Darlington

Darlington 1952, Part II, p. 213.

Diagnosis (*revised*). Rather small (5.7–10.5 mm); narrow *Agonum*-like *or* more or less fusiform; elytra always blotched or mottled with dark and pale; wing-and-seta formula (see Part II, pp. 107ff) + w, ++, (−)(+), −(+)(+) (except *M. seripox* has 3rd intervals with *more* than 3 punctures); last ventral abdominal segment of ♂ more or less emarginate at apex (♂♂ of all species except *scaphipox* now known).

Notes. Six species of this genus were recognized in 1952; 7 more are described below. The following *Key* and list of the 13 species constitutes an informal revision of the whole genus. The number of species is surprising, in view of the fact that they are all winged and that some of them fly (to light). These insects, with their mottled or blotched colorations, may be adapted to live in montane grassland, although the only specimen specifically recorded from such a habitat is the type of *altipox* Darlington (Part II, p. 218), taken in tussock grass above timberline on Mt. Wilhelm.

Key (Revised) to the Species of *Maculagonum*

1. Eyes normal ... 2
– Eyes small but abnormally abruptly prominent ... 11
2. Third intervals of elytra each with several (more than 3) punctures ... *seripox*
– Third intervals 2- or 1-punctate ... 3
3. Third intervals 2-punctate ... 4
– Third intervals 1-punctate ... 7
4. Elytra with pale marks including relatively large pale spots before middle and near suture *c.* 1/4 from apex ... *plagipox*
– Elytra more finely mottled with dark and pale ... 5
5. Prothorax rounded at sides; length over 8 mm ... *pox*
– Prothorax *c.* straight at sides (trapezoidal); length under 7 mm ... 6
6. Less fusiform; head more than 0.80 width prothorax ... *daymanpox*
– More fusiform; head *c.* 0.64 width prothorax ... *scaphipox*
7. Elytra mainly yellow (see also description) ... *tafapox*
– Elytra mainly brown or *c.* equally mixed black or brown and yellow ... 8
8. Small, *c.* 7 mm ... 9
– Larger ... 10
9. Reticulate microsculpture distinct on pronotum and very heavy on elytra ... *altipox*
– Reticulate microsculpture indistinct on pronotum, visible but not heavy on elytra ... *canipox*
10. Posterior-lateral setae of pronotum present; pronotum and base of elytra black ... *atropox*
– Posterior-lateral setae absent; pronotum and base of elytra in part yellow ... *depilapox*
11. Median-lateral setae of pronotum present ... *setipox*
– Median-lateral setae absent ... 12
12. Third intervals of elytra 2-punctate ... *kaindipox*
– Third intervals 1-punctate ... *waupox*

Maculagonum seripox n. sp.

Description. With characters of genus; form as in Figure 49, slender, convex; castaneous, lateral margins and base of prothorax paler, elytra with several rows of testaceous spots sometimes in part irregularly coalescent; reticulate microsculpture faint on head and pronotum, light and somewhat transverse on elytra. *Head* 0.70 and 0.71 width prothorax; eyes normal, moderately large. *Prothorax*: width/length 1.28 and 1.38; base/apex 1.77 and 1.74; margins rather wide (in genus) each with seta-bearing puncture at base, without median-lateral puncture; posterior angles right or slightly obtuse, narrowly rounded. *Elytra*: width elytra/prothorax 1.46 and 1.48; margins *c.* rectangular at humeri; apices rounded, faintly lobed; striae impressed; intervals flat or slightly impressed, 3rd multi-punctate, the punctures often in pale spots and sometimes reduced in number (present posteriorly but not anteriorly). *Secondary sexual characters*: normal; last ventral segment of ♂ moderately emarginate, of ♀ entire. *Measurements*: length *c.* 8.5–10.5 mm; width 2.8–3.5 mm.

Types. Holotype ♂ (Bishop Mus.) from Wau, "Wau Ck.," Morobe Dist., **N-E. N. G.**, 1200–1500 m, Mar. 28, 1963 (Sedlacek). Paratypes: 7 (some in MCZ, Type No. 31839) from Wau and vicinity including Wau Ck. and Mt. Missim, 1200, 1250, 1200–1500, 1450, 1700, 1600–2000 m, dates in Jan., Feb., Mar., June, Sept., 1961–1964 (Sedlaceks), 1 in light trap, 1 in Malaise trap; 1, Edie Ck. (nr. Wau), Bulldog Rd., "Stn. No. 13," 9700 ft. (2960 m), Sept. 20, 1964 (Bacchus, British Mus.).

Additional material (doubtfully identified). **N-E. N. G.**: 1, Wau, Edie Ck., 2100 m, Oct. 7, 1961; 1, Sinofi, 30 km S of Kainantu, 1590 m, Sept. 30, 1959 (T. C. Maa, Bishop Mus.); 1, Daulo Pass (Asaro-Chimbu Div.), 2400 m, June 16, 1955 (Gressitt). **West N. G.**: 1, Star Rge., Bivak 39A, 1500 m, June 30, 1959 (Leiden Mus., Neth. N. G. Exp.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Wau.

Notes. The extra seta-bearing punctures of the 3rd elytral intervals distinguish this from all other known species of the genus. The specimens listed under additional material vary in width of prothoracic margins and in form of elytral apices. More material is needed to show whether more than one species is involved.

Maculagonum pox Darlington

Darlington 1952, Part II, p. 215.

Additional material. **West N. G.**: 1, Star Rge., 1500 m, Bivak 39A, June 30, 1952 (Leiden Mus., Neth. N. G. Exp.).

Notes. The types (including holotype in Leiden Mus.) were from the Snow Mts., **West N. G.**

Maculagonum plagipox Darlington

Darlington 1952, Part II, p. 216.

Description (supplementary). See original description, based on single teneral ♂. Additional material shows color primarily castaneous with sides of prothorax pale-translucent and elytra each with 2 principal yellow spots slightly before middle and *c.* ¼ from apex, each pair of spots sometimes meeting across suture, and with some additional usually smaller yellow spots especially on (but not confined to) intervals 4, 5, and 6. *Prothorax* with posterior angles right or slightly obtuse, slightly blunted. *Elytra* with apices strongly angulate, sometimes subdenticulate.

Additional material. **N-E. N. G.**: 4, Tsenga, Upper Jimmi Valley, 1200 m, July 14, 15, 1955 (Gressitt); 1, Kumur, Upper Jimmi Valley, 1000 m, July 13, 1955 (Gressitt); 3, Karimui, S of Goroka, 1000, 1080 m, June 7, 1961, July 13, 14, 1963 (Sedlaceks), 1 labeled also "Rattan"; 1, Adelbert Mts., Wanuma, 800–1000 m, Oct. 25, 1958 (Gressitt); 1, Pindiu, Huon Pen., 870–1300 m, Apr. 21–22, 1963 (Sedlacek). **West N. G.**: 1, Japen Is., Camp 2 Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Notes. The unique ♂ type (British Mus.) was from the Cyclops Mts., **West N. G.**

Maculagonum daymanpox n. sp.

Description. With characters of genus; form as in Figure 50; color (both individuals slightly teneral) of head, pronotum, and base of elytra brown with prothoracic margins yellowish, elytra except at base nearly evenly mottled brown and testaceous, the testaceous color forming many spots in a brown reticulation, the pattern becoming slightly irregular dorsally *c.* ⅓ from apex; reticulate microsculpture faint on front, light and somewhat transverse on pronotum, heavier and *c.* isodiametric on elytra. *Head* 0.84 and 0.83 width prothorax; eyes normal, rather large, not abruptly prominent. *Prothorax* subquadrate or trapezoidal with base *c.* wide as or slightly wider than width at middle; width/length 1.14 and 1.11 (width measured at middle); base/apex 1.57 and 1.71; lateral margins rather narrow, each with seta at basal angle but without median-lateral setae. *Elytra* ample, slightly narrowed toward base; width elytra/prothorax 1.86 and 1.95; humeral margins slightly (very obtusely) subangulate; apices rounded (faintly lobed); striae entire, groovelike; intervals flat, 3rd 2-punctate. *Secondary sexual characters* normal: last ventral segment of ♂ shallowly but distinctly emarginate, of ♀ entire. *Measurements*: length 6.5–7.0 mm; width 2.5–2.8 mm.

Types. Holotype ♂ (AMNH) and 1 ♀ paratype (MCZ, Type No. 31840) both from Mt. Dayman, Maneau Rge., **Papua**, 2230 m, "N. Slope No. 4," May 19–June 19, 1953 (Geoffrey M. Tate).

Notes. See preceding *Key* for differential characters of this species.

Maculagonum scaphipox Darlington

Darlington 1952, Part II, pp. 215, 220.

Notes. The unique ♀ type (British Mus.), from Orrori, **Papua**, is still the only individual of this species known.

Maculagonum tafapox Darlington

Darlington 1952, Part II, p. 219.

Additional material. **Papua**: 1, Mt. Dayman, Maneau Rge., 2230 m, N Slope No. 4, May 19–June 19, 1953 (Geoffrey M. Tate, AMNH).

Notes. The unique type, from Mt. Tafa, **Papua**, is a ♀. The present specimen, which I compared with the type at the British Museum in April, 1968, is a ♂, with

last ventral segment distinctly but weakly emarginate. Proportions and measurements of this specimen: head/prothorax 0.76; prothoracic width/length 1.29, base/apex 1.39; width elytra/prothorax 1.76; length 6.8 mm, width 2.3 mm.

Maculagonum altipox Darlington

Darlington 1952, Part II, pp. 215, 218.

Notes. This high-altitude species is still known only from the ♀ type (in MCZ) from over 3000 m on Mt. Wilhelm, **N-E. N. G.**, and from subspecies *pallipox* (♂ holotype in Leiden Mus., ♀ paratype in MCZ) from 2800 m on the Snow Mts., **West N. G.**

Maculagonum canipox n. sp.

Description. With characters of genus; form as in Figure 51, small, slender, convex; head blackish, prothorax brown with base broadly and sides narrowly yellowish, elytra irregularly mottled dark brown and yellowish with larger yellowish spot on each elytron behind apical ¾ (these spots nearly meeting across suture) and darker marks coalescent around the pale ones and in irregular zones centering on 3rd intervals; reticulate microsculpture light (faint) on front and pronotum, distinct and *c.* isodiametric on elytra. *Head* 0.74 width prothorax; eyes normal, moderately large. *Prothorax* subquadrate, much narrowed in front, scarcely so behind; width/length 1.22; base/apex 1.56; margins narrow anteriorly, wider posteriorly, each with seta at base, without median-lateral setae. *Elytra* long-oval; width elytra/prothorax 1.68; margins obtuse at humeri; apices independently broadly rounded; striae impressed, slightly irregular; intervals flat or slightly convex, 3rd 1-punctate (puncture in subapical yellow spot). *Secondary sexual characters*: ♂ last ventral segment weakly emarginate; ♀ unknown. *Measurements*: length *c.* 7.0 mm; width 2.4 mm.

Type. Holotype ♂ (Bishop Mus.) from 32 km S of Wau, Morobe Dist., **N-E. N. G.**, Bulldog Rd., 2850 m, May 29–30, 1962 (Sedlacek), Malaise trap; the type is unique.

Notes. See preceding *Key* for differential characters of this small, narrow, convex species.

Maculagonum atropox n. sp.

Description. With characters of genus; form as in Figure 52, suboval, convex; head, prothorax, and base of elytra black except base and lateral margins of prothorax slightly rufescent, elytra finely irregularly mottled dark brown and yellowish with slightly larger yellowish spot *c.* ¼ from apex (and actual apices yellow) and dark color predominant on 3rd and 4th intervals; reticulate microsculpture light on front and pronotum, heavier and *c.* isodiametric on elytra. *Head* 0.74 width prothorax; eyes normal, rather prominent but not abruptly so. *Prothorax* arcuately narrowed anteriorly; width/length 1.17; base/apex 1.79; margins narrow anteriorly, slightly broader posteriorly, each with seta at base but without median-lateral setae; posterior angles obtuse, slightly blunted. *Elytra* ample; width elytra/prothorax 1.79; margins *c.* rectangular at humeri; apices independently broadly rounded; striae fine, impressed; intervals flat, 3rd 1-punctate (puncture in subapical yellow spot). *Secondary sexual characters*: ♂ last ventral segment deeply emarginate, angle of emargination *c.* rectangular; ♀ unknown. *Measurements*: length 8.7 mm; width 3.4 mm.

Type. Holotype ♂ (Bishop Mus.) *c.* 14 km S Edie Ck. (near Wau), **N-E. N. G.**, Bulldog Rd., 2405 m, July 4–10, 1966 (G. A. Samuelson), in light trap; the type is unique.

Notes. This rather large, dark, suboval species too is adequately differentiated in the preceding *Key*.

Maculagonum depilapox n. sp.

Description. With characters of genus; form as in Figure 53; brown, base and (more narrowly) lateral margins of prothorax yel-

lowish, elytra finely mottled with brown and yellow, the yellow color forming a larger common spot less than ¼ from apex, and the dark color coalescent around it; reticulate microsculpture faint on front and pronotum, light and slightly diagonally transverse on elytra. *Head* 0.63 and 0.67 width prothorax; eyes rather large, less prominent than usual. *Prothorax* narrowed anteriorly, scarcely so posteriorly; width/length 1.34 and 1.30; base/apex 1.60 and 1.59; lateral margins moderately wide, without lateral setae; posterior angles slightly obtuse, narrowly rounded. *Elytra* ample; width elytra/prothorax 1.69 and 1.65; humeri right or slightly obtuse; apices irregularly broadly rounded; striae lightly impressed, slightly irregular; intervals *c.* flat, 3rd 1-punctate (puncture in subapical yellow spot). *Secondary sexual characters* normal; ♂ last ventral segment moderately emarginate. *Measurements*: length 8.0–8.4 mm; width 3.2–3.5 mm.

Types. Holotype ♂ (MCZ, Type No. 31843) from Okapa, **N-E. N. G.**, Apr. 27, 1965 (Hornabrook). Paratypes: **N-E. N. G.**: 1, (without head), Okapa, Sept. 16, 1964 (Hornabrook), Umi Simi, 7500 ft. (*c.* 2285 m), "among moss & epiphytes"; 1, Mt. Chapman, 2000 m, May 5, 1966 (Gressitt); 1 (broken), Wau, Edie Ck., 2000 m, Aug. 14, 1963 (P. Shanahan, Bishop Mus.). **Papua**: 1, Mt. Giluwe, 2550 m, May 27, 1963 (Sedlacek). **West N. G.**: 1, Star Rge., 1500 m, Bivak 39A, June 30, 1959 (Leiden Mus., Neth. N. G. Exp.).

Measured specimens: the ♂ holotype and ♀ paratype from Mt. Chapman.

Notes. All specimens agree in lacking posterior- as well as median-lateral prothoracic setae, and they agree well also in other characters given in the *Key* and preceding *Description*.

Maculagonum setipox Darlington

Darlington 1952, Part II, pp. 214, 217.

Notes. Still known only from the unique ♂ type (British Mus.) from Mt. Tafa, **Papua**, 8500 ft. (*c.* 2590 m).

Maculagonum waupox n. sp.

Description. With characters of genus, form as in Figure 54; head, pronotum, and elytra anteriorly black, prothorax only slightly reddish at base and lateral margins, elytra behind base finely mottled blackish and reddish yellow with larger common reddish yellow spot *c.* ¼ from apex; reticulate microsculpture light or faint on front and pronotum, impressed, fine, isodiametric on elytra. *Head* 0.73 and 0.74 width prothorax; eyes moderate in size, abruptly prominent. *Prothorax* widest at or near base, much narrowed anteriorly; width/length 1.18 and 1.16; base/apex 1.92 and 1.82; margins narrow, slightly broader posteriorly, each with seta at base, without median-lateral setae. *Elytra* ample, slightly narrowed anteriorly; width elytra/prothorax 1.74 and 1.74; margins obtusely angulate at humeri; apices independently rounded; striae finely impressed; intervals flat, 3rd 1-punctate (puncture in yellow spot). *Secondary sexual characters* normal; ♂ last ventral segment strongly (*c.* rectangularly) emarginate. *Measurements*: length 7.4–8.5 mm; width 3.1–3.4 mm.

Types. Holotype ♂ (Bishop Mus.) from Wau, Morobe Dist., **N-E. N. G.**, 2400 m, Jan. 9–12, 1962 (Sedlaceks and G. Monteith). Paratypes: 3(2 in MCZ, Type No. 31844) with same data as type; 1, Mt. Kaindi, 16 km SW of Wau, 2200 m, June 8–9, 1962 (Sedlacek), light trap; 1, same locality, 2350 m, Jan. 10, 1962 (Sedlaceks), m. v. light trap. (It seems likely that all specimens including the holotype actually came from Mt. Kaindi, near Wau, above 2000 m).

Measured specimens. The ♂ holotype and a ♀ paratype from Mt. Kaindi.

Notes. See preceding *Key* for this species' distinguishing characters.

Maculagonum kaindipox n. sp.

Description. With characters of genus;

form as in Figure 55; head, pronotum, and base of elytra black, with base of prothorax faintly reddish, elytra behind base irregularly mottled black and reddish with two much larger common yellow spots meeting across suture slightly before middle and *c.* ¼ from apex, the black marks coalescent especially around the posterior yellow spot; reticulate microsculpture absent on front, faint on pronotum, distinct and *c.* isodiametric on elytra. *Head* 0.76 width prothorax; eyes abruptly prominent. *Prothorax* trapezoidal, widest at base; width/length 1.15 (width measured at middle); base/apex 1.74; lateral margins narrow, slightly broader near base, each with seta at base, without median-lateral setae. *Elytra* ample, scarcely narrowed toward base; width elytra/prothorax 1.67; margins at humeri obtuse; apices independently weakly rounded; striae finely impressed; intervals flat, 3rd 2-punctate (punctures in yellow spots). *Secondary sexual characters*: ♂ last ventral segment moderately emarginate; ♀ unknown. *Measurements*: length 6.8 mm; width 2.8 mm.

Type. Holotype ♂ (Bishop Mus.) from Mt. Kaindi (SW of Wau), **N-E. N. G.**, 2350 m, Apr. 30, 1966 (Gressitt); the type is unique.

Notes. Although much like the preceding (*waupox*) and sympatric with it, the present new species seems clearly distinct, being smaller, slightly different in proportions, with 2 rather than 1 conspicuous yellow elytral spots, and with 3rd intervals 2-punctate rather than 1-punctate.

Genus *POTAMAGONUM* Darlington

Darlington 1952, Part II, p. 221.

Diagnosis (*revised*). Large, with long, slender appendages; wing-and-seta formula (see Part II, pp. 107ff) +w, ++, −(−), +++; prothoracic margins wide, translucent; elytral striae conspicuously interrupted; 5th hind-tarsal segments usually with conspicuous accessory setae, but latter sometimes missing (apparently broken off) especially in specimens taken in light traps.

Generic distribution (*revised*). High mountains of much or all of **New Guinea.**

Notes. The 4 species covered by this diagnosis are all listed in the following pages, which constitute an informal revision of the genus. The type species, *P. diaphanum*, was found among wet stones and other cover on the spray-drenched banks of turbulent mountain streams, and this is probably the habitat of the other forms here described.

KEY TO THE SPECIES OF *POTAMAGONUM*

1. Posterior-lateral prothoracic setae present; elytra distinctly aeneous .... *postsetosum*
– Posterior-lateral prothoracic setae absent; elytra brownish black, not distinctly aeneous 2
2. Elytral apices less produced (N-E N. G.) .... *diaphanum*
– Elytral apices more produced, more acute 3
3. Fragments of (interrupted) elytral striae more often linear (Papua) .... *brandti*
– Fragments of elytral striae more often punctiform (West N. G.) .... *julianae*

Potamagonum postsetosum n. sp.

Description. With characters of genus and of type species (below) except as indicated; form as in Figure 56; color as usual except elytra distinctly aeneous. *Head* 0.71 and 0.69 width prothorax; eyes slightly larger and genae slightly shorter than in *diaphanum*. *Prothorax* more evenly rounded and with more broadly rounded posterior angles than in *diaphanum*: width/length 1.28 and 1.32; base/apex not determined because of rounding of angles; lateral margins each with a seta-bearing puncture near outer edge of margin near base. *Elytra*: width elytra/prothorax 1.42 and 1.41; apices slightly acute but not much produced; fragments of (interrupted) elytral striae mostly linear. *Legs*: 5th hind-tarsal segments probably formerly with conspicuous accessory setae, but latter mostly broken off. *Measurements*: length *c.* 13.5–14.5 mm; width 4.7–5.0 mm.

Types. Holotype ♂ (AMNH) and 1 ♀ paratype (MCZ, Type No. 31846) both

from Mt. Dayman, Maneau Rge., **Papua**, 2230 m, "N. Slope No. 4," May 19–June 19, 1953 (Geoffrey M. Tate).

Notes. The presence of posterior-lateral prothoracic setae distinguishes this from all other known members of the genus.

Potamagonum diaphanum Darlington

Darlington 1952, Part II, p. 221.

Additional material. **N-E. N. G.**: 1 Wau, Morobe District, Mt. Missim, 1800 m, Apr. 22, 1966 (Gressitt, Wilkes), Malaise trap; 1, Wau, Nami Ck., 1700 m, June 15, 1962 (Sedlaceks); 1, E Highlands, Purosa, 1700 m, May 17–25, 1966 (Gressitt & Tawi).

Notes. The types (including holotype ♂, MCZ) were from the Chimbu Vy. and Mt. Wilhelm, Bismarck Rge., **N-E. N. G.** The *Additional material* recorded above indicates that the species is widely distributed in the high mountains of N-E. N. G. south of the Ramu-Markham Valley.

Potamagonum brandti n. sp.

Description. With characters of genus and (except as indicated in *Notes* below) of *P. diaphanum.* Color brownish with prothoracic margins testaceous-translucent. *Head* 0.70 and 0.69 width prothorax; details *c.* as in *diaphanum. Prothorax*: width/length 1.19 and 1.22; posterior angles *c.* as in *diaphanum*, more narrowly rounded than in *postsetosum*; lateral margins without setae. *Elytra*: width elytra/prothorax 1.40 and 1.38; apices produced as short spines; (interrupted) striae with fragments short but mostly linear. *Legs*: 5th hind-tarsal segments with well-developed accessory setae. *Measurements*: length *c.* 14.5–15.5 mm; width 4.8–5.0 mm.

Types. Holotype ♀ (Bishop Mus.) and 2 ♀♀ (1 in MCZ, Type No. 31847) all from Goilala, Bome, **Papua**, Owen Stanley Rge., 1950 m, Apr. 30–May 2 (holotype), Mar. 16–31, Apr. 1–15, 1958 (W. W. Brandt).

Measured specimens. The ♀ holotype and 1 ♀ paratype.

Notes. This is very close to *P. diaphanum* (above), differing mainly in having the apical angulations of the elytra more produced, forming short spines. It may prove to be only a geographic subspecies of *diaphanum*, but until more material is available from more localities I prefer to consider it a slightly defined species. The existence of a second, better defined species (*postsetosum*) also in Papua indicates that specific differentiation has occurred in this group in New Guinea.

Potamagonum julianae n. sp.

Description. With characters of genus and (except as indicated in *Notes* below) of *P. diaphanum.* Color brownish black, with prothoracic margins paler-translucent, as usual. *Head* 0.66 width prothorax; details *c.* as in *diaphanum. Prothorax c.* evenly rounded except broadly weakly emarginate anteriorly (as usual); width/length 1.24; lateral margins without setae. *Elytra*: width elytra/prothorax 1.36; apices produced as short acute spines; fragments of (interrupted) striae relatively short, often punctiform (but variable). *Legs*: 5th hind-tarsal segments with conspicuous accessory setae. *Measurements*: length *c.* 14.5 mm; width *c.* 4.9 mm.

Type. Holotype ♀ (Leiden Mus.) from Juliana Bivak, Snow Mts., **West N. G.**, 1800 m, Sept. 8, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. This single specimen probably represents a distinguishable geographic population, but more material is needed to show its characters fully. Perhaps it too (as suggested for *brandti* above) will prove to be a geographic subspecies of *diaphanum*.

Genus *GASTRAGONUM* Darlington

Darlington 1952, Part II, pp. 115, 222.

Notes. Besides additional material of *subrotundum* and *terrestre* (listed below), I have seen three unique specimens in the British Museum that may represent undescribed species of this genus. However, third-stage taxonomic study of the whole

genus, preferably with more material than is now available, will be necessary to establish their distinctness and probable relationships.

Gastragonum subrotundum Darlington

Darlington 1952, Part II, pp. 224, 225.

Additional material. **N-E. N. G.**: 1, Edie Ck. nr. Wau, 2000 m, Oct. 10, 1961 (Sedlacek); 1, Adelbert Mts., Wanuma, 800–1000 m, Oct. 24, 1958 (Gressitt), light trap; 1, Sepalakambang, Salawaket Rge., 1920 m, Sept. 12, 1956 (E. J. Ford, Jr., Bishop Mus.).

Gastragonum terrestre Darlington (and related forms)

Darlington 1952, Part II, pp. 224, 226.

Additional material. Twenty, from various localities mostly in **N-E. N. G.**, at altitudes of 2000 to 2500–2790 m (and 6500, 8600 ft.); specimens in Bishop Mus., CSIRO, and Dept. Agr. Port Moresby.

Notes. These specimens show confusing variation and require third-stage taxonomic treatment, which I cannot give them now. Specimens from near Wau (Edie Ck., Mt. Kaindi, 2000 to 2400 m) may be referable to *terrestroides* Darlington (1952: 227), already recorded from Mt. Mis(s)im.

Genus *IDIAGONUM* Darlington

Darlington 1952, Part II, pp. 114, 229, fig. 10.

Generic distribution (revised). Known from high altitudes (probably usually or always in high-mountain forest) in **West N. G.** (the Snow Mts.) and in western **N-E. N. G.** south of the Ramu-Markham Valley (Bismarck Rge., Bulldog Rd.) and in the adjacent NW corner of **Papua** (Mt. Giluwe).

Notes. This very distinct genus is perhaps not directly related to any other genus in New Guinea. Its origin is undetermined. The 6 known species are all now thoroughly flightless and confined to limited areas at high altitudes. However, the species are closely interrelated, and the different montane populations have perhaps not been long isolated from each other.

Idiagonum asperum Darlington

Darlington 1952, Part II, pp. 230, 231.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 3000 m, July 4, 1955 (Gressitt); 2, Wapenamanda (W Highlands), 2500–2700 m, June 9, 1963 (Sedlacek).

Notes. The Wapenamanda specimens are assigned to this species doubtfully, but they are certainly very close and I do not care to describe them now.

Idiagonum giluwe n. sp.

Description. With characters of genus; form *c.* as in *asperum* Darlington except prothorax slightly broader at base and less angulate at sides; black; head and pronotum dull, elytra moderately shining, microsculpture as described below. *Head* 0.75 and 0.76 width prothorax; eyes small, abruptly prominent (as usual in genus); front finely densely granular. *Prothorax c.* as in *asperum*; width/length 1.14 and 1.17; base/apex 1.05 and 1.05; margins at most weakly angulate near middle; apex margined, base weakly or indistinctly so; disc finely granular (the granules tending to be longitudinal), less strongly (transversely) rugulose than in *asperum*, and with surface especially more finely (longitudinally) rugulose before anterior transverse impression and behind posterior transverse impression. *Elytra*: width elytra/prothorax 1.33 and 1.35; details *c.* as in *asperum*. *Measurements*: length 13.2–14.0 mm; width 4.5–4.9 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Giluwe, (NW corner of) **Papua**, 2500–2750 m, May 30, 1963 (Sedlacek), and 3 paratypes (♂ in MCZ, Type No. 31849, ♂ ♀ in Bishop Mus.) from same locality, 2500, 2800–3280 m, May 30, June 6, 1963 (Sedlacek).

Measured specimens. The ♂ holotype and ♀ paratype.

Notes. Although close to *asperum,* this new species is distinguished by the finer microsculpture of the pronotum, as described above. The prothorax is also slightly wider at base in the new form, but I am not sure the difference is significant.

Idiagonum limatulum n. sp.

Description. With characters of genus; form as in Figure 57, with eyes very abruptly prominent and prothorax wider than in *asperum* and with better defined and more prominent anterior angles; black, relatively shining, microsculpture as described below. *Head* 0.75 and 0.78 width prothorax; front with very fine isodiametric microreticulation and sparse punctulation. *Prothorax*: width/length 1.27 and 1.25; base apex 1.09 and 1.04; margins angulate before middle of length, strongly sinuate before *c.* right posterior angles; apex margined, base irregularly so; disc rather coarsely transversely strigulose, coarsely longitudinally strigulose before anterior transverse impression, coarsely irregularly wrinkled behind posterior transverse impression, with surface of disc somewhat transversely microreticulate rather than finely roughened. *Elytra*: width elytra/prothorax 1.35 and 1.41. *Measurements*: length 13.7–14.0 mm; width 4.0–4.1 mm.

Types. Holotype ♂ (Bishop Mus.) from Wau, Bulldog Rd., **N-E. N. G.**, 2450 m, May 31, 1962 (Sedlaceks), and 1 ♀ paratype (MCZ, Type No. 31850), *c.* same locality ("19–21 km S. of Wau, Bulldog Rd."), 2200–2500 m, May 28, 1962 (Sedlaceks).

Notes. This presumably localized species differs from *asperum,* etc., in being more shining and in having more prominent anterior prothoracic angles.

Genus *MONTAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 233.

Diagnosis (*revised*). Large or medium-sized, somewhat pterostichinelike Agonini; inner wings atrophied, elytra often connate; wing-and-seta formula (see Darlington, Part II, pp. 107ff) –w, ++, (+)(+), (+)(+)(+) (position of lateral prothoracic setae exceptionally variable); mentum toothed, tooth either emarginate (*anax, anassa, nepos*) or entire (other species); outer elytral margins not iterrupted; prosternal process without setae; 5th tarsal segments usually without accessory setae (but these present in *fugitum*); ♂ copulatory organs (Figs. 60A, 63A) typically agonine, with both parameres short and irregularly oval, the left one larger than the right.

Description. No new description required; see preceding *Diagnosis* and (for some significant variations) following *Key to Species.*

Type species. M. toxopeanum Darlington.

Generic distribution (*revised*). Widely distributed on high mountains of **New Guinea.**

Notes. This genus may prove to be polyphyletic and should perhaps be considered temporarily a genus of convenience. The variation in form of mentum tooth and in number and position of prothoracic and elytral setae and punctures is striking, and may eventually give a basis for dividing the genus. However, to divide it now would probably require the recognition of several new monotypic genera, of which the interrelationships would not be known, and which would confuse rather than clarify the situation. Many more species of this group of New Guinean agonines probably remain to be discovered, and making of new genera may well wait until more of them are known.

The following *Key* and list of species constitute an informal revision of all known species of the genus.

KEY TO THE SPECIES OF *MONTAGONUM*

1. Very large, *c.* 20 mm; basal margin of elytra obsolete; 3rd interval of elytra not punctate 2
– Smaller; basal margin of elytra present; 3rd interval of elytra with at least one puncture 3
2. Pronotal margins each with only 1 (median-lateral) seta; elytral margins slightly raised at humeri .... *anax*

– Pronotal margins with additional setae; elytral margins not raised at humeri .... *anassa*
3. Size medium, 13–17 mm; apex of prothorax margined, base not distinctly so 4
– Size smaller 6
4. Third elytral interval with 1 seta-bearing puncture (near apex) .... *nepos*
– Third elytral interval 3-punctate 5
5. Sides of prothorax not sinuate .... *sororcula*
– Sides of prothorax strongly sinuate before base .... *pandum*
6. Prothorax with both base and apex plainly margined .... *filiolum*
– Prothorax with apex plainly but base weakly or not margined 7
7. Sides of prothorax broadly (not strongly) reflexed .... *fugitum*
– Sides of prothorax scarcely reflexed .... *toxopeanum*

Montagonum anax n. sp.

Description. With characters of genus; form as in Figure 58, very large, heavily built; black, appendages dark; moderately shining, reticulate microsculpture fine, isodiametric on front, in part slightly transverse on pronotum, slightly irregular but nearly isodiametric on elytra. *Head* 0.84 width prothorax; eyes small, *c.* ½ long as genae behind them and not breaking outline of sides of head (diameter of head is measured across genae rather than across eyes in this case); mandibles very long, almost straight for much of length, moderately arcuate apically; mentum with deeply emarginate tooth; palpi long, slender. *Prothorax*: width/length 1.27; base/apex 0.79; lateral margins moderate, somewhat broader posteriorly, well reflexed, each with one seta-bearing puncture on inner face (not edge) slightly before middle, without basal punctures; base and apex not margined; disc with fine middle line, usual transverse impressions (the posterior deeper), and poorly defined baso-lateral impressions, impunctate. *Elytra* connate; width elytra/prothorax 1.27; margin obsolete at base except near humeri, raised and obtusely angulate at humeri, not interrupted before apex; subapical sinuations slight, apices rather narrowly irregularly rounded; positions of striae irregularly impressed with very fine incomplete irregular impressed lines at bottom; intervals slightly convex, 3rd without dorsal punctures, outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment broadly emarginate, not lobed. *Secondary sexual characters*: ♂ front tarsi with 3 segments (irregularly) 2-seriately squamulose, middle tarsi not squamulose; ♂ with 1 seta-bearing puncture each side apex last ventral segment; ♂ copulatory organs as described under genus (but not fully hardened and too distorted to draw); ♀ unknown. *Measurements*: length 20.5 mm; width 7.3 mm.

Type. Holotype ♂ (Bishop Mus.) from Murray P(ass), **Papua**, 2800 m, Nov. 6, 1965 (Sedlaceks); the type is unique.

Notes. See preceding *Key to Species* and notes under following species for comparison. This is one of the finest of all the agonines of the world.

Montagonum anassa n. sp.

Description. With characters of genus; form (Fig. 59) virtually as in preceding species (*anax*) and characters the same except as follows. *Head* 0.85 width prothorax. *Prothorax*: width/length 1.30; base/apex 0.84; lateral margins each with seta slightly before middle of length (as in *anax*), an additional seta midway between median-lateral one and apex, and a seta on margin just before base (subbasal seta present on right side, but left side broken at this point). *Elytra*: width elytra/prothorax 1.29; margin not raised at humeri; otherwise *c.* as in *anax*. *Secondary sexual characters*: ♀ with 2 setae each side last ventral segment; ♂ unknown. *Measurements*: length 20.0 mm; width 7.1 mm.

Type. Holotype ♀ (MCZ, Type No. 31852), from Mt. Yule, Central Dist., **Papua**, 10,700 ft. (*c.* 3260 m), Sept. 1963 (D. Hutton & M. Stevens), "alpine grass zone"; the type is unique.

Notes. This species may be a geographic representative of the preceding (*anax*),

but the difference in prothoracic setae is striking and unexpected.

Montagonum nepos n. sp.

Description. With characters of genus; form as in Figure 60, *c.* as in *anax* but with head relatively narrower and prothorax less narrowed behind; black, appendages dark; reticulate microsculpture fine, *c.* isodiametric on head, slightly transverse on disc of pronotum and elytra. *Head* 0.75 and 0.71 width prothorax; form *c.* as in *anax* but eyes slightly larger, *c.* long as genae behind them; mentum tooth deeply emarginate. *Prothorax*: width/length 1.12 and 1.18; base/apex 0.90 and 0.96; lateral margins narrow (somewhat variable), moderately explanate, each with seta-bearing puncture at or slightly before middle of length but none at base; apex finely margined, base not margined; disc irregularly rather weakly impressed, with baso-lateral impressions shallow, irregular, not distinctly punctate. *Elytra*: width elytra/prothorax 1.22 and 1.26; base margined, margin obtusely angulate or narrowly rounded at humeri; subapical sinuations of margins subobsolete, apices narrowly rounded into suture; striae slightly impressed, impunctate; intervals slightly convex, 3rd with 1 seta-bearing puncture far back (on declivity), often on outer edge of interval (puncture present on both sides of all specimens but position slightly variable), outer intervals not modified apically. *Lower surface* virtually impunctate (abdominal segments in part longitudinally slightly rugulose); abdomen not pubescent. *Legs* as described for *anax*. *Secondary sexual characters*: ♂ front as well as middle tarsi apparently without squamae; ♂ probably usually with 1, ♀ 2 setae each side last ventral segment (in fact the single ♂ has 1 puncture on the left but 2 on the right side); ♂ copulatory organs as in Figure 60A. *Measurements*: length *c.* 17.5 mm; width 5.9–6.1 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Kaindi (near Wau, Morobe Dist.), **N-E. N. G.**, 2350 m, Jan. 12, 1962 (Sedlaceks); 1 ♀ paratype (MCZ, Type No. 31853), Bulldog Rd., 19–29 km S of Wau, 2200–2500 m, May 31, 1962 (Sedlacek).

Additional material. One ♀ (Bishop Mus.), Mt. Kaindi, 2350 m, July 12, 1963 (Sedlacek), m. v. light trap.

Measured specimens. The ♂ holotype and ♀ paratype.

Notes. This well-characterized species is adequately distinguished from others in the preceding *Key to Species*. The specimen listed under *Additional material*, though from the same locality as the holotype, has wider prothoracic margins and differs slightly in other ways, and may prove to be a separate species.

Montagonum sororcula n. sp.

Description. With characters of genus; form as in Figure 61; black, prothoracic margins slightly reddish-translucent, appendages dark reddish; reticulate microsculpture fine, isodiametric on front, somewhat transverse on disc of pronotum, more transverse on elytra. *Head* 0.65 width prothorax; eyes *c.* long as and more prominent than genae; mandibles rather long, scarcely arcuate except at apex; mentum tooth triangular, entire. *Prothorax*: width/length 1.12; base/apex 1.13; lateral margins moderately wide, scarcely wider posteriorly, moderately reflexed, each with seta-bearing punctures before middle and well before base (position shown in Fig. 61); apex conspicuously margined, base vaguely so; disc with median impressed line distinct, transverse impressions subobsolete, basolateral impressions weak, poorly defined, vaguely subpunctate. *Elytra*: width elytra/prothorax 1.35; base margined, margin obtuse at humeri, subapical sinuations weak, apices narrowly rounded; striae impressed, not distinctly punctulate; intervals slightly convex, 3rd 3-punctate, outer intervals not modified apically. *Lower surface* impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segments emarginate, not lobed. *Secondary sexual characters*: ♂ unknown; ♀ with 2 or 3 (unsymmetric) setae each

side last ventral segment. *Measurements*: length 13.0 mm; width 4.8 mm.

Type. Holotype ♀ (Bishop Mus.) from Murray P(ass), **Papua**, 2400–2800 m, Nov. 6, 1965 (Sedlaceks); the type is unique.

Notes. See preceding *Key to Species* for place of this among other *Montagonum*.

Montagonum pandum n. sp.

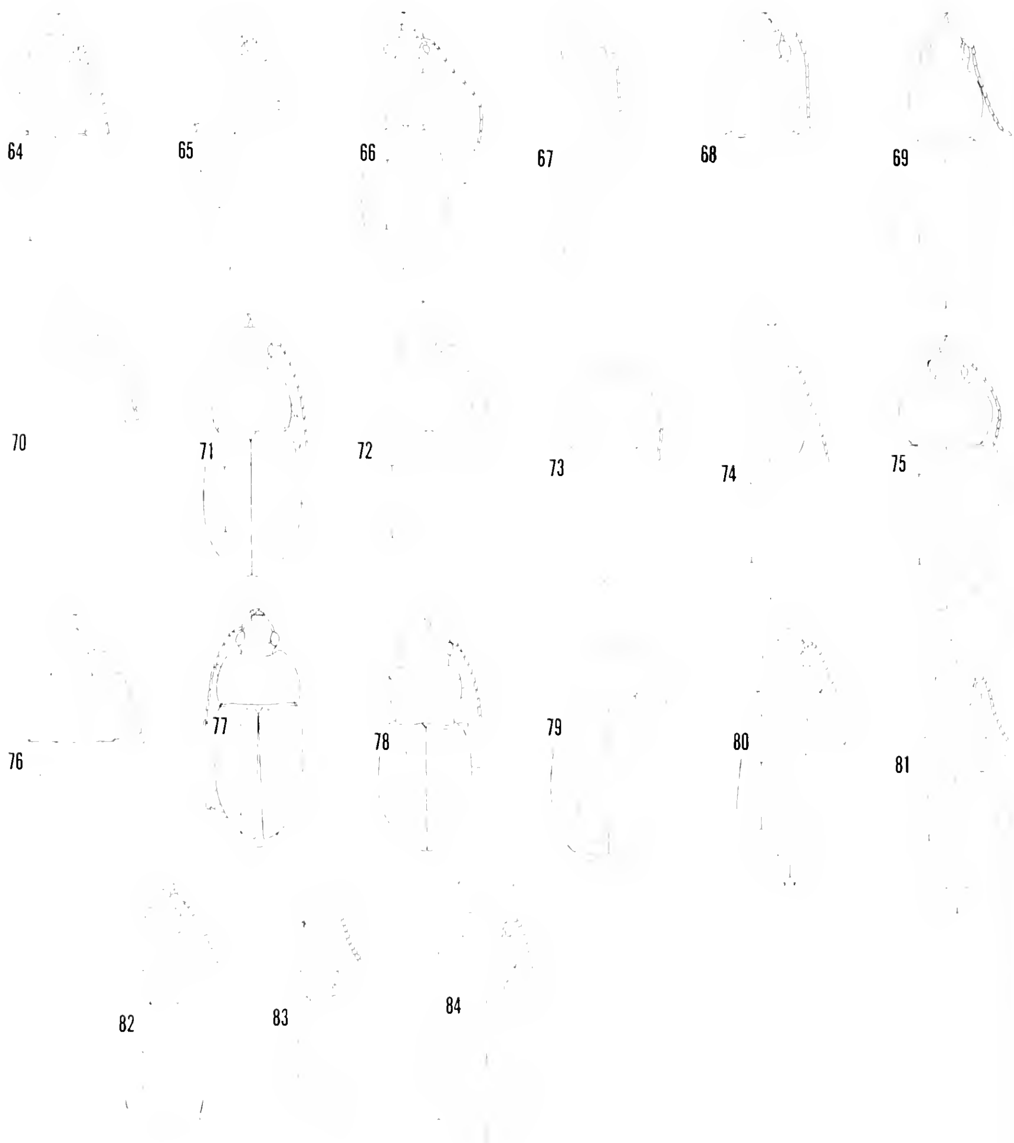
Description. With characters of genus; form as in Figure 62; black, margins of prothorax slightly reddish translucent, appendages dark; reticulate microsculpture fine, isodiametric on front, slightly transverse on pronotum, more transverse on elytra. *Head* 0.67 and 0.68 width prothorax; eyes small, slightly shorter than genae behind them but more abruptly prominent than usual; mandibles rather long, weakly arcuate; mentum tooth entire, triangular. *Prothorax*: width/length 1.08 and 1.15; base/apex 1.07 and 1.05; sides abruptly sinuate *c*. ⅙ of length before base, then subparallel to narrowly rounded basal angles; lateral margins moderate, moderately reflexed, each with seta-bearing puncture between ¼ and ⅓ from base (2 punctures close together at this point on one side of one specimen) but without other lateral setae; apex conspicuously margined, base inconspicuously or weakly so; disc with fine middle line, weak transverse impressions, shallow poorly defined faintly punctulate baso-lateral impressions. *Elytra*: width elytra/prothorax 1.33 and 1.27; base margined, margin *c*. rectangular (slightly obtuse) at humeri, where outer margin slightly raised; subapical sinuations broad, slight; apices narrowly rounded; striae entire, well impressed, not or faintly punctulate; intervals slightly convex, 3rd 3-punctate (position of punctures as usual in Agonini); outer intervals not modified apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs c*. as in *anax*. *Secondary sexual characters*: ♂ front (not middle) tarsi slightly dilated, 3 segments biseriately squamulose; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements*: length 15.5–16.8 mm; width 5.5–6.1 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Chapman, **N-E. N. G.**, 2000 m, May 5, 1966 (collector not given); and 1 ♂ paratype (MCZ, Type No. 31855) from Bulldog Rd., 2200–2500 m, May 31, 1962, **N-E. N. G.**, 19–29 km S of Wau (Sedlacek).

Notes. This species is unique in the genus in the abrupt sinuation of the sides of the prothorax and especially in the position of the lateral prothoracic setae. Other differential characters are given in the *Key to Species*.

Montagonum fugitum n. sp.

Description. With characters of genus; form as in Figure 63, slender *Calathus*-like, with base of prothorax broadly emarginate at middle; dull black, margins of prothorax slightly reddish translucent, legs reddish, antennae brown; reticulate microsculpture fine, isodiametric (in part) on front, irregular but not strongly transverse on pronotum and elytra. *Head* 0.58 width prothorax; eyes rather small but more abruptly prominent than usual; mandibles rather short, blunt, scarcely arcuate; mentum tooth narrow-triangular, entire. *Prothorax*: width/length 1.12 (length measured at middle as usual); base/apex 1.42; lateral margins narrow anteriorly, running into broad slightly depressed areas posteriorly, each with seta-bearing puncture slightly before base just inside marginal bead, without median-lateral setae; apex conspicuously margined, base not or at most vaguely so (base partly broken); disc weakly convex, middle line distinct, transverse impressions vague, posterior-lateral impressions shallow, not well defined, impunctate. *Elytra*: width elytra/prothorax 1.29, base margined, margin *c*. rectangular (slightly arcuate) at humeri, with humeral margins slightly raised in front of angle; subapical sinuations virtually obsolete, apices narrowly rounded; striae moderately impressed, entire, not punctate; intervals slightly convex, 3rd 3-punctate (punctures placed as usual in



Figures **64–84** (see text, section [15]): **64**, *Montagonum filiolum* n. sp., ♂ holotype; **65**, *M. toxopeanum* Darl., ♂ paratype; **66**, *Nebriagonum foedum* n. sp., ♀ para.; **67**, *Laevagonum pertenue* n. sp., ♀ para.; **68**, *L. frustum* n. sp., ♀ holo.; **69**, *L. giluwe* n. sp., ♀ holo.; **70**, *Fortagonum bufo* Darl., ♀, Swart Vy.; **71**, *F. antecessor* n. sp., ♀ holo.; **72**, *F. oodinum* n. sp., ♀ holo.; **73**, *F. okapa* n. sp., ♂ para., Mt. Elandora; **74**, *F. formiceps* n. sp., ♂ holo.; **75**, *F. hornabrooki* n. sp., ♂ para., Wau; **76**, *F. distortum* n. sp., ♀ holo.; **77**, *Oodes terrestris* n. sp., ♂ para., Dobodura; **78**, *Chydaeus hinnus* n. sp., ♀ holo.; **79**, *Physodera bacchusi* n. sp., ♂ holo.; **80**, *Demetrida parena* n. sp., ♀ holo.; **81**, *Hexagonia gressitti* n. sp., ♂ holo.; **82**, *Colasidia papua* n. sp., ♀ holo.; **83**, *C. madang* n. sp., ♀ holo.; **84**, *Helluopapua cheesmani* n. sp., ♂ holo.

Agonini), outer intervals not modified apically. *Lower surface* virtually impunctate (except sides of mesosternum vaguely subpunctate); abdomen not pubescent. *Legs* slender; hind tarsi with all segments sulcate each side above; 4th hind-tarsal segment long, shallowly emarginate, not lobed; 5th segment with *c.* 3 conspicuous accessory setae each side. *Secondary sexual characters*: ♂ with front (not middle) tarsi slightly dilated, biseriately squamulose; ♂ with 1 seta each side last ventral segment; ♂ copulatory organs as in Figure 63A; ♀ unknown. *Measurements*: length *c.* 11 mm; width 4.0 mm.

Type. Holotype ♂ (MCZ, Type No. 31856) from Mt. Amagwiwa, nr. Wau, Morobe Dist., **N-E. N. G.**, *c.* 11,000 ft. (*c.* 3350 m) Sept. 24, 1963 (Guy Rosenberg), in alpine grass zone; the type is unique.

Notes. Although I am tentatively placing this interesting species in *Montagonum*, in order to avoid premature multiplication of genera, it has nothing to do directly with any other species now placed in that genus. I think it may be an independent derivative of *Altagonum*, although it is ruled out of that "genus of convenience" by atrophy of the wings and resultant shortening of metepisterna (which are slightly longer than wide) and superficial fusion of elytra. The presence of conspicuous accessory setae on the 5th tarsal segments differentiates *fugitum* from all *Altagonum*, and indeed from all other *Montagonum*.

Montagonum filiolum n. sp.

Description. With characters of genus; form as in Figure 64; black, appendages dark brownish; reticulate microsculpture light and *c.* isodiametric on front, irregularly transverse on pronotum and elytra. *Head* 0.71 and 0.69 width prothorax; eyes moderate, slightly longer than and more prominent than genae; mandibles moderate (somewhat shorter and more arcuate than in most other species of genus); mentum tooth triangular, blunted but not distinctly emarginate. *Prothorax*: width/length 1.20 and 1.27; base/apex 1.21 and 1.19; margins narrow, slightly wider basally, each with seta-bearing punctures slightly before middle and virtually at basal angle; base and apex conspicuously margined; disc with usual moderate impressions, basolateral impressions moderate, poorly defined, vaguely subpunctate. *Elytra*: width elytra/prothorax 1.32 and 1.28; base margined, margin obtuse at humeri, not specially elevated at humeri; subapical sinuations subobsolete, apices rather narrowly rounded to suture; striae lightly impressed, not distinctly punctate; intervals slightly convex, 3rd 3-punctate (punctures placed as usual in Agonini); outer intervals not specially modified apically. *Lower surface* virtually impunctate; abdomen not pubescent (but segments 2–4 swollen at middle). *Legs*: 4th hind-tarsal segment short, deeply emarginate, scarcely lobed; 5th segments without obvious accessory setae. *Secondary sexual characters*: ♂ front (not middle) tarsi slightly dilated, with 3 segments biseriately squamulose; ♂ with 1, ♀ 2 setae each side last ventral segment. *Measurements*: length *c.* 10–11 mm; width 3.8–4.0 mm.

Types. Holotype ♂ (MCZ, Type No. 31857), and 3 paratypes (♂♀ Dept. Agr. Port Moresby, ♀ MCZ) all from Mt. Albert-Edward, Central Dist., **Papua**, 13,000 ft. (3660 m), Aug. 30, 1963 (F. H. A. Kleckham & I. G. Pendergast), under stones in alpine grass zone.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Another very distinct species, differentiated in the preceding *Key to Species*.

Montagonum toxopeanum Darlington

Darlington 1952, Part II, p. 234.

Notes. Still known only from the types (holotype ♂ in Leiden Mus.) from Letterbox Camp, Snow Mts., **West N. G.**, 3600 m.

Genus *NEBRIAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 235.

Generic distribution (*revised*). Slopes of Mt. Wilhelm, Bismarck Range, **N-E. N. G.** (5 species), with 1 Mt. Wilhelm species extending to Mt. Otto; 1 Mt. Wilhelm stock represented by 1 or more endemic forms SE to the vicinity of Okapa; and 1 doubtfully related species on the Snow Mts., **West N. G.**; all at rather high altitudes, 1 species reaching *c.* 4300 m on Mt. Wilhelm (Darlington, Sedlacek).

Notes. The variation of characters and ecology of the species of this genus is discussed in Part II. The occurrence of a slightly differentiated endemic form, described below, in a cave on the Porol Range extends the ecologic as well as the geographic distribution of the genus.

Nebriagonum cephalum Darlington

Darlington 1952, Part II, pp. 238, 239.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 4250 m, June 3, 1963 (Sedlacek).

Notes. Mt. Wilhelm is, of course, the type locality of the species, which ranges up to *c.* 4300 m on the mountain.

Nebriagonum foedum n. sp.

Description. With characters of genus; form as in Figure 66, virtually as in *N. cephalum* Darlington; dull black, appendages dark; reticulate microsculpture fine, isodiametric on front, transverse on pronotum, more transverse (scarcely distinct) on elytra where visible. *Head* 0.92 and 0.90 width prothorax; eyes small but rather abruptly prominent; 2 setae over each eye. *Prothorax*: width/length 1.00 and 0.99; base/apex 1.01 and 1.00; lateral margins narrow, somewhat wider posteriorly, apparently without lateral setae; base and apex margined; disc normally impressed, baso-lateral impressions slight, impunctate. *Elytra* oval; width elytra/prothorax 1.55 and 1.58; base margined, margins obtuse at humeri; apical sinuations slight or obsolete; apices independently rounded (♂) or angulate or subdenticulate *c.* in line of 3rd intervals (♀); striae deep, impunctate or faintly punctulate; intervals moderately convex, apparently without dorsal punctures (see *Notes* below). *Lower surface, inner wings, legs,* and *secondary sexual characters* normal; 4th hind-tarsal segment lobed, outer lobe longer than inner; 5th segments without obvious accessory setae. *Measurements*: length *c.* 9.5 mm; width *c.* 3.3 mm.

Types. Holotype ♂ (MCZ, Type No. 31858) and 2 ♀♀ paratypes all from Maimbobo Cave, North Dumam, Porol Rge., **N-E. N. G.**, Sina Sina, Nov. 15, 1965 (F. Parker), in fruit bat droppings.

Additional material. **N-E. N. G.**: 1 ♂, Okapa, Purosa, 6500 ft. (*c.* 1980 m), 1965 (Hornabrook), under stone in stream bed.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The 3 types are so coated with fruit bat guano, which I have been unable to remove satisfactorily, that I cannot be sure that the lateral prothoracic setae and dorsal elytral punctures are lacking. The heads of all specimens are completely clean, so there can be no question about the supraocular setae being present on both sides in all specimens, but the pronota and elytra are completely coated except where I have scraped small areas bare with a pin point. Characters visible in spite of the coating, however, show that this new species is in general similar to *Nebriagonum cephalum* Darlington (above) but different in having deeper elytral striae and differently formed elytral apices, and probably also in lacking lateral prothoracic and dorsal elytral seta-bearing punctures. The prothorax is slightly longer in *foedum* than in *cephalum*, but not as long as in *percephalum* Darlington (Part II, p. 240), from which the new species differs also in possessing both pairs of supraocular setae (anterior pair lacking in *percephalum*).

Although the ♂ holotype has rounded and the 2 ♀♀ paratypes denticulate elytral apices, I think the difference is probably individual rather than sexual. The ♂ from Okapa has elytral apices strongly denticulate on a slightly different pattern from the Maimbobo Cave ♀♀ and may prove to

represent a separate population, but extent of variation should be established before it is formally described.

Nebriagonum transitum Darlington

Darlington 1952, Part II, pp. 238, 241.

Additional material. **N-E. N. G.**: 20, Mt. Wilhelm (incl. L. Aunde and L. Strunki), 2800–2900, 3400–3500 m, dates in June, July, 1963 (Sedlacek); 10, Mt. Otto including summit (on Bismarck Rge. SE of Mt. Wilhelm), Nov. 1965 (collector not given, Dept. Agr. Port Moresby).

Notes. I found this species (the types) common on Mt. Wilhelm both in the highest mountain forest and above the forest on open grassy slopes.

Genus *LAEVAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 243.

Diagnosis (revised). Small (4.8–8.5 mm) *Europhilus*- or *Calathus*- or cistellidlike; body smooth in outline (no sharp angles), smoothly convex; pronotum with basolateral fovea absent or weak; wing-and-seta formula (see Part II, p. 107) –w, ++, (–)–, ––(–); 4th hind-tarsal segments variable, simply emarginate or long-lobed in different species.

Generic distribution (revised). Known only from the Bismarck Range, **N-E. N. G.**, and Mt. Giluwe just across the border in NW **Papua**.

Notes. To this genus, previously known from 4 species, I am now adding 3 more. They differ mainly in characters of form and proportions best shown by drawings (Figs. 67–69) rather than by a new key. Besides those actually recorded, I have seen a single specimen from Mt. Giluwe, Papua (Bishop Mus.), which might be referred to *L. citum* Darlington (Part II, p. 245) but is so much broader that it may prove to represent a separate species.

Laevagonum cistelum Darlington

Darlington 1952, Part II, pp. 245, 246.

Additional material. **N-E. N. G.**: 3, Daulo Pass (Asaro-Chimbu Div., Bismarck Rge.), 2400 m, June 16, 1955 (Gressitt).

Laevagonum pertenue n. sp.

Description. With characters of genus; form as in Figure 67, very slender; brown, head and pronotum blackish, appendages brown; reticulate microsculpture isodiametric on front, transverse on pronotum and elytra. *Head* 0.78 and 0.77 width prothorax. *Prothorax*: width/length 0.91 and 0.96; base/apex 1.48 and 1.42; lateral margins fine, slightly wider toward base, without setae; base inconspicuously margined, apex with margin interrupted at middle; disc with middle line and slight transverse impressions and broad poorly defined basolateral areas scarcely impressed but slightly irregular or subpunctate. *Elytra*: width elytra/prothorax 1.54 and 1.55; base margined, margin *c.* right (slightly acute) at humeri; subapical sinuations slight, apices independently rather narrowly rounded; striae light, slightly irregular but not distinctly punctulate; intervals almost flat, 3rd with 1 seta-bearing puncture posteriorly (near top of declivity); outer intervals partly impressed and irregular toward apex. *Legs*: 4th hind-tarsal segment with 2 long nearly equal lobes. *Measurements*: length *c.* 7.5–8.5 mm; width 2.5–2.8 mm.

Types. Holotype ♂ (Bishop Mus.) from Daulo Pass (Asaro-Chimbu Div., Bismarck Rge.), **N-E. N. G.**, 2400 m, June 16, 1955 (Gressitt), and 1 ♀ paratype (MCZ, Type No. 31859) from Mt. Wilhelm, Bismarck Rge., 3000 m, July 4, 1955 (Gressitt).

Notes. The presence of a (posterior) seta-bearing puncture on the 3rd interval, the long-lobed 4th hind-tarsal segments, and the very slender form distinguish this species from *citum* Darlington and all other previously known species of *Laevagonum*.

Laevagonum frustum n. sp.

Description. With characters of genus; form as in Figure 68, very small, with short,

rounded elytra; brownish black, appendages yellowish brown; reticulate microsculpture light, isodiametric on front, somewhat transverse on pronotum, more transverse on elytra. *Head* 0.73 and 0.75 width prothorax. *Prothorax*: width/length 1.20 and 1.13; base/apex 1.19 and 1.20; lateral margins narrow, scarcely wider posteriorly, without setae; base and apex finely margined; disc with middle line, slight transverse impressions, baso-lateral impressions distinct but irregular, not or vaguely punctate. *Elytra*: width elytra/prothorax 1.58 and 1.61; base margined, margin very obtuse (virtually rounded) at humeri; subapical sinuations broad, apices independently rounded; striae slightly impressed, irregular but not distinctly punctulate; intervals flat or very weakly convex, 3rd without punctures, outer intervals not impressed toward apex. *Legs*: 4th hind-tarsal segment with rather long lobes, outer lobe longer than inner. *Secondary sexual characters* of ♂ unknown, of ♀ normal. *Measurements*: length *c.* 4.8–5.0 mm; width 2.1–2.2 mm.

Types. Holotype ♀ (Bishop Mus.) from Daulo Pass (Asaro-Chimbu Div., Bismarck Rge.), **N-E. N. G.**, 2400 m, June 16, 1955 (Gressitt); 1 ♀ paratype (Bishop Mus.) with same data except June 15; 1 ♀ paratype (MCZ, Type No. 31860), same data except 2500 m, June 12.

Measured specimens. The ♀ holotype and first ♀ paratype.

Notes. The small size and very stout form distinguish this from *cistelum* Darlington and from all other known species of the genus, and the long-lobed 4th hind-tarsal segments differentiate it also from all other species except *pertenue* (above).

Laevagonum giluwe n. sp.

Description. With characters of genus; form as in Figure 69; irregular dark brown, suture and appendages in part more rufous; reticulate microsculpture slightly irregular, *c.* isodiametric on front and elytra, slightly transverse on pronotum. *Head* 0.69 width prothorax. *Prothorax* rounded-quadrate; width/length 1.17; base/apex *c.* 1.18 (angles too rounded for exact measurement); lateral margins fine, without setae; apex margined, base not margined at middle; disc rather weakly *c.* evenly convex, with fine middle line, transverse impressions vague, baso-lateral impressions absent, surface slightly irregular baso-laterally but scarcely punctate. *Elytra*: width elytra/prothorax 1.36; base margined, margins obtusely angulate at humeri; subapical sinuations absent; apices independently rounded; striae slightly impressed, faintly (hardly distinctly) punctulate; intervals *c.* flat, 3rd without dorsal punctures. *Secondary sexual characters* of ♂ unknown, of ♀ normal. *Measurements*: length 7.0 mm; width 2.6 mm.

Type. Holotype ♀ (Bishop Mus.) from Mt. Giluwe, NW **Papua**, 3750 m, May 29, 1961 (J. L. & M. Gressitt), in forest patch; the type is unique.

Notes. This new species is intermediate in form between *citum* Darlington and *cistelum* Darlington, being broader than *citum* (and without the denticulate elytra of that species) but less cistelid-like and with relatively wider head than *cistelum.*

Although the occurrence of this insect on Mt. Giluwe extends the range of *Laevagonum* to Papua, the actual distance is not great.

Genus *FORTAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 247.

Diagnosis (revised). Moderate-sized (8.8–13.5 mm), heavily built, broadly subparallel or fusiform Agonini; wing-and-seta formula (see Part II, p. 107) –w, (–)(+), –(–), (–)(–)(–). (The only species of the genus in which anterior supraocular setae are present is *distortum*, under which see, below.)

Type species. Fortagonum fortellum Darlington.

Generic distribution (revised). High mountains of **New Guinea.**

Notes. Fortagonum may have been derived at high altitudes on New Guinea from

an ancestor or ancestors (the genus may be polyphyletic) something like "*Altagonum*" *bigenum* (p. 299), which is excluded from *Fortagonum* only by its full wings. *Fortagonum* is probably not directly related to *Montagonum* (p. 308), which has probably had a separate origin (or origins) on the same mountain ranges. Both these two genera are heavily built and flightless, but they differ not only in presence (in *Montagonum*) and absence (in *Fortagonum*) of anterior supraocular setae but also in form, most *Montagonum* being *Pterostichus*-like, most *Fortagonum* more agonine in appearance. In fact, the phylogeny of these and other high-mountain Agonini in New Guinea is likely to have been much more complex than second-stage taxonomy can show.

Five species were originally included in *Fortagonum*, and 6 more are added now. The following *Key* and list of species constitute an informal revision of the whole genus. However, many more species probably remain to be discovered on different mountain summits in New Guinea. Judging from their diverse form and the diverse modifications of the eyes and mandibles, some of the species probably have special habits or special foods, so that their biology is likely to be interesting.

KEY (REVISED) TO THE SPECIES OF *FORTAGONUM*

1. Both pairs supraocular setae lacking; form very broadly rounded-fusiform (Fig. 70) .... *bufo*
– At least posterior supraocular setae present; form variable but never so broadly rounded 2
2. Margins of pronotum relatively narrow anteriorly, although very broad posteriorly 3
– Prothoracic margins very broad anteriorly as well as posteriorly 9
3. Mandibles normal, moderately long and arcuate 4
– Mandibles slender, virtually straight 7
4. Pronotum with posterior-lateral setae 5
– Pronotum without posterior-lateral setae 6
5. Form normal; pronotal margins moderately reflexed .... *antecessor*
– Form depressed; pronotal margins very wide but scarcely reflexed .... *oodinum*
6. Prothoracic width/length *c.* 1.40 or more; elytra weakly iridescent .... *fortellum*
– Prothoracic width/length *c.* 1.25 or less; pronotum and especially elytra strongly iridescent .... *okapa*
7. Form normal, subparallel; relatively wider (prothoracic width/length 1.28 and 1.35) .... *forceps*
– Form subfusiform, narrowed at least anteriorly 8
8. More fusiform; prothoracic width/length 1.27 .... *cychriceps*
– Subfusiform, more narrowed anteriorly than posteriorly; prothoracic width/length 1.11 .... *formiceps*
9. Eyes *c.* normal, front not swollen .... *hornabrooki*
– Eyes abruptly prominent and/or front conspicuously swollen 10
10. Eyes very abruptly prominent; front only slightly modified; only posterior supraocular setae present .... *limum*
– Eyes less abruptly prominent; front conspicuously swollen posteriorly; 2 pairs supraocular setae present (placed as indicated in Fig. 76) .... *distortum*

Fortagonum bufo Darlington

Darlington 1952, Part II, pp. 248, 252.

Additional material. **West N. G.**: 1 ♀, Swart Vy., W ridge, 1800–2000 m, Nov. 19, 1958 (Gressitt).

Notes. This species was described from Mist Camp, Snow Mts., **West N. G.**, at 1800 m. The Swart Valley specimen agrees well with the ♀ paratype in the MCZ.

Fortagonum antecessor n. sp.

Description. With characters of genus; form as in Figure 71; black, prothoracic margins and appendages slightly reddish; reticulate microsculpture fine, *c.* isodiametric on front, irregular and slightly transverse on disc of pronotum and elytra. *Head* 0.60 width prothorax; eyes moderate; posterior supraocular setae present; mandibles rather short and arcuate (in genus); front almost evenly convex. *Prothorax*: width/length 1.35; base/apex 1.51; lateral margins narrow anteriorly, much broader posteriorly, moderately explanate, each with seta-bearing puncture near posterior angle; apex margined and with anterior angles

only moderately advanced (in genus); base slightly broadly emarginate, not margined; disc with middle line and weak transverse impressions; baso-lateral impressions formed mainly by troughs between disc and margins, in part vaguely subpunctate. *Elytra*: width elytra/prothorax 1.27; base margined, margin *c.* right (slightly obtuse) at humeri; subapical sinuations almost obsolete, apices independently rounded; striae impressed, not punctate; intervals slightly convex, 3rd normally 3-punctate, outer intervals not much modified toward apex, no 10th intervals. *Lower surface* in part slightly wrinkled or vaguely subpunctate. *Legs*: 4th hind-tarsal segment apparently emarginate but not lobed (in poor condition); 5th hind-tarsal segment with distinct but not large accessory setae. *Secondary sexual characters*: ♀ with 2 seta-bearing punctures each side last ventral segment; ♂ unknown. *Measurements*: length *c.* 9.0 mm; width *c.* 3.7 mm (specimen not in condition to measure accurately).

Type. Holotype ♀ (MCZ, Type No. 31862) from Mt. Albert-Edward, Central Dist., **Papua**, 12,000 ft. (3660 m), Aug. 30, 1963 (F. H. A. Kleckham & I. G. Pendergast), in alpine grass zone, under stone; the type is unique.

Notes. This species has approximately the form of *F. fortellum* and may resemble the ancestral stock of that and of related species. It (the present new species) differs from *fortellum* in having posterior-lateral prothoracic setae present, anterior angles of prothorax less advanced, and humeral angles less acute, all these characters being perhaps relatively primitive or unspecialized.

Fortagonum oodinum n. sp.

Description. With characters of genus; form as in Figure 72, with head very small and prothorax and anterior portion of elytra more depressed than usual; black, legs dark, tarsi and antennae more reddish; reticulate microsculpture isodiametric on front, transverse on pronotum, scarcely distinct on elytra which faintly iridescent in some lights. *Head* 0.46 and 0.46 width prothorax; eyes moderate; posterior supraocular setae present; mandibles moderately long and moderately arcuate (in genus). *Prothorax* large, wide, and flatter than usual; width/length 1.50 and 1.51; base/apex 1.87 and 1.73 (sic); lateral margins very wide especially posteriorly but scarcely explanate, separated from weakly convex disc by distinct but shallow poorly defined channels ending posteriorly in poorly defined baso-lateral impressions, each with seta-bearing puncture at base somewhat in from edge of margin; apex margined, base not margined at middle; disc with slightly impressed middle line and weak transverse impressions with basal and lateral areas vaguely subpunctate. *Elytra*: width elytra/prothorax 1.09 and—(right elytron missing); base margined, margin *c.* right (slightly arcuate) at humeri; subapical sinuations slight or obsolete; striae well impressed, not punctulate; intervals slightly convex, 3rd finely 3-punctate (punctures placed as usual in Agonini), outer intervals (7, 8) deeply impressed apically; narrow apparent 10th interval present behind middle. *Lower surface* not much punctate. *Legs*: 4th hind-tarsal segments long, shallowly emarginate, not lobed; 5th segments without distinct accessory setae. *Secondary sexual characters*: ♂ unknown; ♀ with 2 setae each side last ventral segment. *Measurements*: length *c.* 9.5–10.0 mm; width *c.* 4.0–4.2 mm.

Types. Holotype ♀ (Bishop Mus.) from Bulldog Rd., **N-E. N. G.**, 2500 m, May 31, 1962 (no collector given); and 1 (broken) ♀ paratype (MCZ, Type No. 31863) from Bulldog Rd., 29 km SW of Wau, 2500 m, Feb. 15, 1962.

Notes. This species is superficially somewhat similar to a terrestrial oodine. It is probably related to *Fortagonum fortellum* Darlington but differs in being broader and more depressed, with smaller head, and with a distinct seta-bearing puncture on each side of base of pronotum. However, this puncture may sometimes be present in *fortellum* (see below).

Fortagonum fortellum Darlington

Darlington 1952, Part II, pp. 248, 251.

Additional material. **Papua**: 1 ♂, Murray P(ass), 2400–2800 m, Nov. 6, 1965 (Sedlaceks).

Notes. This specimen agrees in general and in proportions with the type series from the Bismarck Range, **N-E. N. G.**, the proportions of the Murray Pass ♂ being *head* 0.53 width prothorax; *prothorax*, width/length 1.42 and base/apex 1.69; and *elytra*, width of elytra/prothorax 1.21. However, the Murray Pass individual differs from the types of *fortellum* in having a seta-bearing puncture on each side of the pronotum on the face (not edge) of the margin near the posterior angle—the actual setae are missing (broken off) but punctures mark their positions. More material is needed to show whether these punctures characterize a distinguishable population, or whether they vary individually. I have re-examined the 28 specimens of the type series of *fortellum* still at the MCZ and find no lateral prothoracic setae or punctures in any of them. However, the dorsal elytral punctures do vary remarkably in *fortellum*, as orginally noted.

Fortagonum okapa n. sp.

Description. With characters of genus; form as in Figure 73, nearly as in *fortellum* but with prothorax narrower, more narrowed anteriorly, and with anterior angles more produced; black, strongly iridescent especially on elytra, appendages dark, tarsi and outer segments of antennae paler brown; reticulate microsculpture faint or unresolved (at 80×) on most of upper surface. *Head* 0.52 and 0.50 width prothorax; eyes moderate; posterior supraocular setae present; mandibles moderate and moderately arcuate (in genus). *Prothorax*: width/length 1.18 and 1.25; base/apex 1.62 and 1.62; lateral margins wide, very wide posteriorly, moderately explanate, without seta-bearing punctures; apex margined, base not; disc with middle line impressed, transverse impressions subobsolete, baso-lateral impressions continuous with (obtuse) marginal gutters, not distinctly punctate. *Elytra*: width elytra/prothorax 1.20 and 1.20; base margined (margin sometimes hidden under base of prothorax), margin acutely angulate at humeri (more acute than in *fortellum*); subapical sinuations obsolete, apices *c.* conjointly rounded except narrowly rounded into suture; striae impressed, not punctulate; intervals slightly convex (more convex posteriorly), 3rd 3-punctate (punctures minute, difficult to see, but present on both sides in all specimens), outer intervals very convex but not compressed and not impressed toward apex, 10th intervals absent or indistinct. *Lower surface* in part slightly punctate. *Legs*: 4th hind-tarsal segments emarginate, scarcely lobed; 5th segments without accessory setae. *Secondary sexual characters* normal. *Measurements*: length *c.* 10.3–12.5 mm; width 4.2–4.8 mm.

Types. Holotype ♂ (MCZ, Type No. 31864) and 2 paratypes (Hornabrook Coll.) from Okapa, Purosa, **N-E. N. G.**, 7000 ft. (2135 m), Nov. 29, 1965 (Hornabrook); and 2 additional paratypes (MCZ and Hornabrook Coll.) from Mt. Elandora, **N-E. N. G.**, Oct. 15, 1965 (Hornabrook).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Okapa.

Notes. The present new species probably represents *fortellum* of the Bismarck Range but differs in form (as indicated at the beginning of the present description) and is much more iridescent. The long type series of *fortellum* showed remarkable variation in some characters including modification of the apices of the 7th and 8th striae, but this variation probably does not occur in *okapa*: the intervals in question are strongly convex in all the 5 specimens listed above, with no sign of impressions on any of them.

Fortagonum forceps Darlington

Darlington 1952, Part II, pp. 248, 249.

Notes. Still known only from Moss Forest Camp, Snow Mts., **West N. G.**, 2600–2800 m.

Fortagonum cychriceps Darlington

Darlington 1952, Part II, pp. 248, 250.

Notes. The still-unique type is from Mist Camp, Snow Mts., **West N. G.**, 1800 m.

Fortagonum formiceps n. sp.

Description. With characters of genus; form as in Figure 74, more narrowed anteriorly than posteriorly, with exceptionally long slender mandibles; opalescent black, legs dark, antennae more reddish; reticulate microsculpture light and *c.* isodiametric on front, not resolved at 80× on pronotum and elytra. *Head* 0.62 width prothorax; eyes small, rather abruptly prominent; posterior supraocular setae present, well behind level of eyes; mandibles long, slender, very weakly arcuate; front almost evenly convex except for shallow sublongitudinal frontal impressions. *Prothorax*: width/length 1.11; base/apex 1.41; lateral margins narrow anteriorly, much broader posteriorly, weakly explanate, without seta-bearing punctures (an apparent puncture near basal angle on left side is probably a nonsetose impression); base not margined, apex with margin interrupted at middle; disc with impressed middle line, transverse impressions virtually obsolete, baso-lateral impressions rather wide, weak, vaguely subpunctate. *Elytra*: width elytra/prothorax 1.31; base finely margined, margin acutely angulate at humeri; subapical sinuations obsolete; apices *c.* conjointly rounded; striae well impressed, not punctulate; intervals slightly convex, 3rd impunctate, outer intervals not modified apically, no 10th intervals. *Lower surface* not distinctly punctate. *Legs*: 4th hind-tarsal segments shallowly emarginate, not lobed; 5th segments without distinct accessory setae. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c.* 11.0 mm; width 4.0 mm.

Type. Holotype ♂ (Bishop Mus.) from Swart Vy., **West N. G.**, W ridge 1800–2000 m, Nov. 19, 1958 (Gressitt); the type is unique.

Notes. The long, slender, nearly straight mandibles relate this species to *forceps* and *cychriceps.* Comparison with the paratype of the former in the MCZ shows that the present new species differs in having smaller eyes and narrower prothorax with narrower margins. Comparison with the description of *cychriceps* shows even greater differences, the new species having a relatively wider head (only 0.48 width prothorax in *cychriceps*) and narrower prothorax (width/length 1.27 in *cychriceps*). The unusual form of the mandibles in these 3 species suggests specialized feeding behavior worth looking for in the field.

Fortagonum hornabrooki n. sp.

Description. With characters of genus; form as in Figure 75, with exceptionally wide, widely margined prothorax; black, elytra purplish, appendages dark, tarsi and antennae slightly browner; reticulate microsculpture fine, *c.* isodiametric on front, somewhat transverse on disc of pronotum, more transverse on elytra. *Head* 0.50 and 0.49 width prothorax; eyes moderately abruptly prominent; mandibles moderately long, moderately arcuate; front slightly irregular but not strikingly convolved; posterior supraocular setae present. *Prothorax*: width/length 1.68 and 1.76; base/apex 1.48 and 1.47; lateral margins very wide anteriorly and even wider posteriorly, rather weakly reflexed anteriorly, slightly more reflexed posteriorly, each with seta at extreme base on the denticulate angle; apex with anterior angles advanced, finely margined; base subtruncate, finely margined; disc weakly convex, with usual impressions weak, baso-lateral impressions formed mainly by explanate margins, base and posterior-lateral impressions vaguely subpunctate. *Elytra*: width elytra/prothorax 1.10 and 1.06; base margined, margin rather narrowly rounded at humeri; subapical sinuations moderate, apices each irregularly rather narrowly rounded, almost sub-

angulate; striae impressed, not distinctly punctate; intervals slightly convex, 3rd 3-punctate, outer intervals not much modified apically, no 10th interval. *Lower surface* not or not much punctate. *Legs*: 4th hind-tarsal segments moderately lobed, outer lobe longer than inner; 5th segments without accessory setae. *Secondary sexual characters* of ♂ normal; of ♀ unknown. *Measurements*: length 11.8–13.5 mm; width 4.6–5.0 mm.

Types. Holotype ♂ (MCZ, Type No. 31866) from Okapa, **N-E. N. G.**, May 14, 1965 (Hornabrook); 1 ♂ paratype, same locality, Aug. 18, 1965 (Hornabrook, in his collection); 1 ♂ paratype (Bishop Mus.), Wau, Nami Ck., 1750 m, Aug. 6, 1963 (Sedlaceks).

Measured specimens. The ♂ holotype and the ♂ paratype from Wau.

Notes. In width of prothorax and of prothoracic margins, this species is comparable only with *limum* and *distortum* (below), but the present species lacks striking modifications of the eyes and front. It is a fine species, and I take pleasure in naming it for the collector, in recognition of his success in finding remarkable new Carabidae in New Guinea, especially in the mountains.

Fortagonum limum Darlington

Darlington 1952, Part II, p. 248.

Notes. The unique type, from Mt. Mis(s)im, Morobe Dist., **N-E. N. G.**, is still the only individual known, but the following new species (*distortum*) is probably closely allied.

Fortagonum distortum n. sp.

Description. With characters of genus; form as in Figure 76, very wide, convex; black, elytra faintly purplish, lateral margins of prothorax broadly reddish-translucent, legs dark, antennae brown; reticulate microsculpture isodiametric on posterior part of head, transverse on pronotum, transverse (in part indistinct) on elytra. *Head* 0.50 and 0.50 width prothorax; eyes rather small, rather abruptly prominent (but genae *c*. evenly long-oblique behind them), separated from front by deep channels; mandibles moderate and moderately arcuate (in genus); front distorted, broadly and strongly swollen posteriorly, the swollen area deeply channeled at middle; *both* pairs supraocular setae present. *Prothorax* very broad, very broadly margined; width/length 1.74 and 1.71; base/apex 1.47 and 1.58; lateral margins moderately explanate, each with seta-bearing puncture at basal angle; apex conspicuously margined, base finely so; disc with middle line well impressed, transverse impressions slight, baso-lateral impressions weak; disc vaguely subpunctate at base and sides. *Elytra* very wide and short; width elytra/prothorax 1.10 and—(1 elytron broken off, although mounted with specimen); base margined, margin rounded at humeri; subapical sinuations broad, slight; apices narrowly independently rounded; striae rather lightly impressed, not or indistinctly punctulate; intervals barely convex, 3rd apparently impunctate, outer intervals not much modified toward apex, 10th intervals indistinct. *Lower surface* in part (not including proepisterna) more or less wrinkled or subpunctate. *Legs*: 4th hind-tarsal segments short, rather deeply emarginate, slightly lobed, outer lobe longer than inner; 5th segments without obvious accessory setae. *Secondary sexual characters* of ♂ unknown, of ♀ normal. *Measurements*: length *c*. 10.5–11.5 mm; width *c*. 5.0–5.5 mm.

Types. Holotype ♀ (MCZ, Type No. 31867) from Offafina, Okapa, **N-E. N. G.**, Nov. 12, 1964 (Hornabrook); and 1 broken ♀ paratype (Bishop Mus.) from Kainantu, **N-E. N. G.**, 2250 m, Jan. 8, 1965 (Sedlacek).

Notes. This remarkable species is generally similar in form and appearance to *limum* but differs in structure of head: in the ♀ type of *limum*, the eyes are more abruptly prominent but the front is not swollen, and *limum* lacks the anterior supraocular setae which are present in *distortum*. The relationships of these two species are

so obvious that I am placing *distortum* in *Fortagonum* in spite of presence of anterior supraocular setae. In modification of head these two species of *Fortagonum* resemble the unrelated (lebiine) *Dolichoctis distorta* Darlington (1968, Part III, p. 127), suggesting parallelism either of adaptations or of genetic processes.

Tribe PERIGONINI

Darlington 1968, Part III, p. 5.

This and the following tribes have been treated so recently by me that I have little or nothing to add in most cases.

Genus *PERIGONA* Castelnau

Darlington 1968, Part III, p. 6.

Notes. I have seen 39 additional specimens of *Perigona* from New Guinea. They include some new locality records (which cannot be given here) but no new species and no important new material of poorly known species.

Tribe LICININI

Genus *DICROCHILE* Guérin

Darlington 1968, Part III, p. 16.

Dicrochile gigas Castelnau

Castelnau 1867, Notes on Australian Coleop., p. 66.
Sloane 1923, Proc. Linnean Soc. New South Wales, 48: 36.

Description. None required here; see following *Notes.*

Types. Described from Rockhampton, Brisbane, and the Clarence R., all in south Queensland or northern New South Wales in eastern **Australia**. Since this species is primarily Australian, selection of a lectotype should await study of Australian material. I did *not* find types of this species in the museum at Melbourne in 1957.

Occurrence in New Guinea. **Papua**: 1, Rouku, Morehead R., (opposite the tip of Cape York), Apr. 1962 (W. W. Brandt, CSIRO).

Notes. In my key to New Guinean *Dicrochile* (1968) the present species runs to *acuta* Darlington, which in fact may prove to be a small New Guinean form of *gigas*. Specimens of *acuta* measure from *c.* 12.5 to *c.* 15.5 mm; Australian specimens of *gigas*, *c.* 20 mm or more. The individual from Rouku measures 19.5 mm and may represent an extension of the Australian population to southern Papua.

Tribe CHLAENIINI

Genus *CHLAENIUS* Bonelli

Darlington 1968, Part III, p. 20.

Notes. I have seen 376 additional specimens of *Chlaenius* from New Guinea. They all represent more or less common species of which the occurrence and gross distribution in New Guinea has been adequately stated. Only a few of the detailed locality records are worth listing here. No additional species of the genus have been found near Wau.

Chlaenius maculiger Castelnau

Darlington 1968, Part III, p. 25.

Additional material. **West N. G.**: 4, Waigeo Is., Camp 2 (Buffelhorn), June 1938 (Cheesman), 1 of these specimens labeled also "at light."

Tribe OODINI[1]

Genus *ANATRICHIS* Leconte

Anatrichis pusilla Sloane

Darlington 1968, Part III, p. 32.

[1] An endemic species of the primarily Australian genus *Coptocarpus* has been found at Dumun, **N.-E. N. G.**, 7500–8000 ft. (*c.* 2300–2400 m), Aug. 21, 1967 (Fred Parker), but was received too late to be described in the present paper. It is *not* included in my statistical analysis of the New Guinean carabid fauna. It has atrophied wings, as have all the Australian species, but the genus is presumably derived from a winged ancestor.

Additional material. **West N. G.**: 3, River Tor (mouth), 4 km E of Hol Maffen, July 19, 1959 (T. C. Maa, Bishop Mus.).

Genus *OODES* Bonelli

Oodes exiguus Andrewes

Darlington 1968, Part III, p. 33.

Additional material. **West N. G.**: 2, River Tor (mouth), 4 km E of Hol Maffen, July 19, 1959 (T. C. Maa, Bishop Mus.).

Oodes terrestris n. sp.

laevissimus Andrewes 1924, Ann. Mag. Nat. Hist. (9), 14: 588 (not *laevissimus* Chaudoir 1882).
Darlington 1968, Part III, pp. 33, 34.

Description. Form as in Figure 77; parallel-sided, slightly more depressed than usual; black, appendages dark; shining, but upper surface very finely (irregularly isodiametrically) reticulate and minutely punctulate. *Head* 0.51 and 0.51 width prothorax; clypeus not margined, without seta-bearing punctures; labrum with 6 separate setae, the inner ones smaller but not clumped; anterior supraocular punctures absent, posterior present. *Prothorax*: width/length 1.70 and 1.70; base/apex 1.80 and 1.77; a seta on basal edge each side near angle; disc with middle line extremely fine, basal impressions very shallow and poorly defined. *Elytra*: width elytra/prothorax 1.07 and 1.06; base margined; striae very fine on disc, deeper laterally, finely punctulate especially laterally; intervals flat on disc, 3rd with 2 small punctures near middle and at or behind apical ¼. *Inner wings* full in some, slightly reduced in other individuals. *Lower surface*: sides especially of meso- and metasterna finely closely punctate; prosternal process not margined between coxae. *Secondary sexual characters*: ♂ front tarsi moderately dilated, 2nd segment slightly wider than long, 3 segments densely squamulose below; ♂ with 1, ♀ 2 setae each side before apex last ventral segment. *Measurements*: length 11.5–13.3 mm; width 4.6–5.7 mm.

Types. Holotype ♂ (MCZ, Type No. 31868) and 21 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and additional paratypes as follows. **Papua**: 1, Kokoda, 1200 ft. (366 m), Aug. 1933 (Cheesman). **N-E. N. G.**: 19, Aitape, Aug. 1944 (Darlington); 7, lower Busu R., Huon Pen., Apr. 4, May 13, 1955 (E. O. Wilson, MCZ); 2, Erima, Astrolabe Bay, 1897 (Biró); 1, Sattelberg (British Mus.); 2, Wareo, Finschhafen (Rev. L. Wagner, South Australian Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. A specimen of this species in the Andrewes Collection (British Museum) is identified as *laevissimus* Chaudoir and marked as compared with type. Comparison with this specimen led me in 1968 to misidentify the present species and redescribe the true *laevissimus* as *longior* (see below). The present species is a very distinct one, recognizable by parallel-sided, depressed form and by technical characters given in my previous key (Part III, pp. 32–33). It differs from most other species of the genus in that it occurs in leaf litter on the floor of rain forest rather than in or beside swamps or pools. It is the base species of what must now be called the *terrestris* group of *Oodes*, characterized in my key (referred to above), and including *O. rossi* Darlington and *O. wilsoni* Darlington, both of which seem to be -w, flightless derivatives of *terrestris*-like stock.

Oodes laevissimus Chaudoir

Chaudoir 1882, Ann. Soc. Ent. France, ser. 6, 2: 361.
Andrewes 1930, Cat. Indian Carabidae, p. 313 (*Simous*).
longior Darlington 1968, Part III, p. 38 (NEW SYNONYMY).

Description. See under *Oodes longior* Darlington 1968.

Types. A large ♂ (which I now designate as lectotype) and a smaller ♀ specimen both labeled "Nuova Guinea Fly River ' L. M. D'Albertis 1876–77," and "Ex Museo Chaudoir."; in Oberthür Coll. (Box 191), Paris Mus. (seen).

Occurrence in New Guinea. Known only from the 2 types (above), from **Papua**, and from the types of *longior* from Hollandia, **West N. G.**, and Ambunti, Sepik R., **N-E. N. G.**

Notes. For explanation of my (1968) misidentification of this species, see under *Oodes terrestris* (above).

Tribe HARPALINI

Darlington 1968, Part III, p. 38.

This tribe includes some of the commonest Carabidae in New Guinea. Much additional material of some of the species has come to hand, but I shall record here only one obviously new species and a few important new records. The number of additional specimens in this tribe *not* recorded below is 249.

Genus *CHYDAEUS* Chaudoir

Darlington 1968, Part III, p. 47.

Chydaeus hinnus n. sp.

Description. Doubtfully assigned to this genus (see following *Notes*); form as in Figure 78, strongly convex; black, epipleurae and appendages browner; dull, reticulate microsculpture close, isodiametric on front, slightly transverse on pronotum, slightly more transverse on elytra. *Head* 0.79 width prothorax; eyes rather small, separated from mouth below by *c.* ½ their diameter; mentum toothed; ligula free at apex, narrow, 2-setose; paraglossae curved, slightly longer than ligula, separate from it; 2nd segment labial palpi plurisetose. *Prothorax* cordate; width/length 1.24; base/apex 1.06; lateral margins fine, each with seta *c.* ¼ from apex; base weakly finely margined, apex not margined at middle; disc with short impressed middle line, very weak transverse impressions, virtually no basolateral impressions, irregularly inconspicuously punctulate across basal area. *Elytra* narrowed toward base; width elytra/prothorax 1.26; humeri subdentate; apices rather strongly sinuate; striae entire, moderately impressed, impunctate; 3rd intervals without dorsal punctures. *Inner wings* vestigial, reduced to scales that scarcely extend beyond metasternum. *Lower surface* and *legs* without obvious special characters. *Secondary sexual characters*: ♀ with 2 setae each side last ventral segment; ♂ unknown. *Measurements*: length *c.* 8.7 mm; width 3.4 mm.

Type. Holotype ♀ (MCZ, Type No. 31869) from Okapa (Kamira), **N-E. N. G.**, May 11, 1965 (R. Hornabrook); the type is unique.

Notes. In the absence of the ♂, I cannot be sure that this species is a *Chydaeus.* But the species is an interesting one, which should be described, so that collectors will look for it in the future. It is surely different from anything previously known in New Guinea. It differs from *Chydaeus papua* Darlington (Part III, p. 47) in being smaller and smoother, with relatively narrower prothorax and less punctate pronotum.

Genus *TRICHOTICHNUS* Morawitz

Darlington 1968, Part III, p. 48.

Notes. Of this genus, I have seen 232 additional specimens from New Guinea. Besides a number of relatively common species, the new material includes some specimens that cannot be satisfactorily placed now and that may represent new forms, but which are not sufficiently distinct to describe without third-stage study. No species, other than those previously recorded, have been found at or near Wau.

Genus *EGADROMA* Motschulsky

Darlington 1968, Part III, p. 69.

Notes. Of the common species of this genus, 118 additional specimens have been seen.

Egadroma cyclops Darlington

Darlington 1968, Part III, p. 70.

Additional material. **Papua**: 3, Brown

R., May 25, 1956 (E. J. Ford, Jr., Bishop Mus.), in light trap.

Notes. The unique type is from the Cyclops Mts., near Hollandia, **West N. G.** I see now that this species is similar to and probably represents *E. rectifrons* Bates, which is recorded from SE Asia, Sumatra, and Borneo, and is represented in the Philippines (Leyte, series in MCZ, possibly distinguishable from true *rectifrons*) but not in Australia. However, the New Guinean individuals have the elytral apices more strongly sinuate than in my few specimens of true *rectifrons*.

Tribe LEBIINI

Darlington 1968, Part III, p. 80.

Two new genera have been added to the New Guinean list since Part III went to press. The following insertions to my *Key to Genera of Lebiini of New Guinea* (Part III, pp. 81ff) should facilitate their identification. The species concerned are, of course, treated below, with a few additional important new records, including one of a *Lebia* previously unknown from New Guinea. Besides the individuals recorded under other headings below, I have seen 220 additional specimens of this tribe from New Guinea.

(INSERTIONS FOR KEY TO GENERA OF *LEBIINI* OF NEW GUINEA)

5. Form characteristic, *either* as in Fig. 42 (1968) *or* Fig. 79 (present paper); upper surface *either* coarsely rugose and pubescent *or* sparsely pubescent chiefly at sides of elytra and anterior angles of prothorax ... 5a
– Not described in one or more details ... 6
5a. Upper surface coarsely rugose and pubescent; form as in Fig. 42 (1968) ... *Lachnoderma*
– Upper surface not coarsely rugose, pubescence sparse and restricted; form as in Fig. 79 ... *Physodera*
11. [Characters of *Somotrichus*]
– Not as above in one or more ways ... 11a
11a. Form and color (head and prothorax yellow, elytra dark blue) of minute *Brachinus*; length *c.* 5 mm ... *Omobrus*
– *Either* form *or* color different ... 12

Genus *LEBIA* Latreille

Darlington 1968, Part III, p. 85.

Notes. Two species of *Lebia* are to be added to the number listed from New Guinea by me in 1968. One has been recorded before but was overlooked by me in 1968. The other has recently been discovered on the island. Fifteen additional specimens of previously recorded species have been seen but need not be listed in detail.

Lebia papuensis Macleay

Macleay 1876, Proc. Linnean Soc. New South Wales, 1: 167.
Sloane 1917, Proc. Linnean Soc. New South Wales, 42: 424.

Description (from Macleay). Apparently a *Lebia* of typical form; reddish-testaceous becoming brown on elytra "which have an indistinct black fascia near the apex"; prothorax short-transverse, probably of usual *Lebia* form; elytra broad, flat, sinuate-truncate, strongly striate with intervals broad and convex; length 3 lines (*c.* 6 mm).

Type. From Hall Sound (south coast of **Papua**); presumably in Macleay Coll., Sydney (not seen).

Occurrence in New Guinea. Known with certainty only from the type.

Notes. This may prove to be a senior synonym of *Lebia papuella* Darlington (Part III, p. 88), but *papuella* is usually smaller and does not have the indistinct black fascia called for in the description of *papuensis*.

Lebia melanonota Chaudoir

Chaudoir 1870, Bull. Soc. Nat. Moscow, 43, Part 2, p. 226, t. 1, f. 45.
Csiki 1932, Coleop. Cat., Carabidae, Harpalinae 7, p. 1325 (see for synonymy and additional references).
Louwerens 1956, Treubia, 23: 225.

Description. A large *Lebia*; reddish yellow, elytra with broad black median stripe covering 4 inner intervals each side of suture and extending from base to less than ¼ from apex; prothorax transverse-

subcordate (not hemispheric); outer angles of elytra rounded; length *c.* 8 mm.

Type. From Moreton Bay (Brisbane), **Australia**; type in Oberthür Coll., Paris Mus. (not seen).

Occurrence in New Guinea. **Papua**: Rouku, Morehead R., West Papua, Apr. 1962 (W. W. Brandt, CSIRO).

Notes. This species is now known from eastern **Australia**, **New Guinea**, the **Solomons** (specimens in MCZ), **Moluccas** (Halmahera Is., Louwerens, 1956), **Java** (Andrewes Coll., British Mus.), and the **Lesser Sundas** (Adonare Is.).

The large size and broad black median elytral stripe immediately distinguish *melanonota* from all species of *Lebia* previously known from New Guinea. Regardless of its distribution elsewhere, the occurrence of *melanonota* at Rouku in southern Papua suggests a recent extension from Australia.

Genus *PHYSODERA* Eschscholtz

Eschscholtz 1829, Zool. Atlas, p. 8.
Csiki 1932, Coleop. Cat., Carabidae, Harpalinae 7, p. 1346 (see for additional references and list of species).
Jedlicka 1963, Ent. Abhandlungen, 28: 296, 300.

Diagnosis. Form characteristic (Fig. 79); surface in part very sparsely pubescent (at sides of elytra, and more conspicuously at front angles of prothorax); 4th hind-tarsal segments deeply emarginate. See preceding *Supplementary Key to Genera.*

Description. None required here.

Type species. Physodera dejeani Eschscholtz.

Generic distribution. The SE corner of **Asia** to the **Philippines**, **Celebes**, and **New Guinea** (not Australia).

Notes. The new species described below constitutes the first record for this genus from New Guinea, and sets the eastern limit of the generic distribution.

Physodera bacchusi n. sp.

Description. With characters of genus (above); form as in Figure 79, broad, elytra relatively convex; head and pronotum black, slightly reddish in part, elytra black slightly aeneous each with small subapical red spot near suture, lower surface irregularly reddish black, appendages black; shining, reticulate microsculpture indistinct. *Head* 0.75 width prothorax; front flattened, slightly irregularly impressed each side and middle between eyes. *Prothorax*: width/length 2.06; base/apex 1.63; lateral margins broad, broadly reflexed, each with group of hairs at basal angle (including 1 special seta near base) and more longer hairs anteriorly; disc with deep middle line coarse to base, irregular transverse impressions, baso-lateral impressions deep but scarcely distinct from posterior ends of marginal troughs; surface irregularly punctate across base and on margins. *Elytra*: width elytra/prothorax 1.67; striae entire, punctulate but not otherwise deeply impressed; intervals almost flat, 3rd with several inconspicuous seta-bearing punctures mostly on inner edge, and 5th and 7th each with a few such punctures in part near middle of width of intervals. *Lower surface* scarcely punctate but in part (especially abdomen) sparsely pubescent. *Inner wings* fully developed. *Legs*: 4th hind-tarsal segments broad, very deeply emarginate, with long broad lobes; claws each with *c.* 6 teeth. *Secondary sexual characters*: ♂ front tarsi with 3 segments very narrowly biseriately squamulose; ♂ middle tibiae slightly bent out toward apex but not otherwise modified; ♂ with 1 principal seta each side last ventral segment; ♀ unknown. *Measurements*: length 12.0 mm (to apex elytra); width 6.0 mm.

Type. Holotype ♂ (British Mus.) from Finisterre Rge., **N-E. N. G.**, Damanti, 3550 ft. (1083 m), "Stn. No. 30," Oct. 2–11, 1964 (M. E. Bacchus); the type is unique.

Notes. Of previously described species, this is probably nearest to *P. cyanipennis* v. d. Poll (known to me only from the description, 1889, Notes from Leyden Mus. 11, p. 253) of Celebes, but the color is different (*cyanipennis* has elytra dark blue with violet reflections, and without red spots), and the median line of the pronotum

is obsolete in *cyanipennis* but deeply impressed in *bacchusi.*

Genus *MINUTHODES* Andrewes

Darlington 1968, Part III, p. 95.

Notes. Besides the individual of *sedlacekorum* recorded below, I have seen 70 additional specimens of commoner species of this genus from New Guinea.

Minuthodes sedlacekorum Darlington

Darlington 1968, Part III, p. 97.

Additional material. **N-E. N. G.**: 1, Okapa (Okasa), July 8, 1965 (Hornabrook), "pine forest."

Notes. The unique type is from Wau. The present specimen agrees with it structurally but has the pale elytral markings forming 3 more nearly continuous fasciae.

Genus *CATASCOPUS* Kirby

Darlington 1968, Part III, p. 101.

Notes. Seventy-five additional New Guinean specimens of this genus have been examined, in addition to those recorded below.

Catascopus sidus Darlington

Darlington 1968, Part III, p. 105.

Additional material. **N-E. N. G.**: 4, Okapa (Okasa), Sept. 29, 1964 (Hornabrook).

Notes. Variation in color of this species is noted under the original description. The present specimens are entirely green above, except for coppery areas behind the humeri. Color may prove to distinguish geographic populations of the species in different parts of New Guinea, but much more material is necessary to delimit them.

Genus *COPTODERA* Dejean

Darlington 1968, Part III, p. 110.

Notes. Additional New Guinean specimens of this genus examined total 108.

Genus *DOLICHOCTIS* Schmidt-Goebel

Darlington 1968, Part III, p. 124.

Notes. One hundred forty additional specimens of *Dolichoctis* have been examined from New Guinea but need not be listed in detail.

Genus *OMOBRUS* Andrewes

Andrewes 1930, Zool. Mededeelingen Mus. Leiden, 13: 199.
Van Emden 1937, Stettiner Ent. Zeitschrift, 98: 41.
Jedlicka 1963, Ent. Abhandlungen, 28: 299, 431.

Diagnosis. See under tribe Lebiini (above), insertion for key to genera of tribe. Form of minute *Brachinus* but abdomen with only 6 visible ventral segments and mandibles without setae in scrobes; 4th hind-tarsal segments only emarginate (not lobed); claws simple.

Description. None required here.

Type species. O. praetextus Andrewes (below).

Generic distribution. See under following species.

Notes. Andrewes originally assigned this genus to the tribe Brachinini, but this was surely wrong. The insect does look like a small *Brachinus*, but its technical characters are wholly different. It is in fact a member of the Lebiini, as stated by Van Emden. The latter's assignment of it to a place among the Dromii is at least reasonable, although further study is needed to decide its exact relationships.

Omobrus praetextus Andrewes

Andrewes 1930, Zool. Mededeelingen Mus. Leiden, 13: 200.
Jedlicka 1963, Ent. Abhandlungen, 28: 431, Pl. 4, Fig. 30.

Description. With characters of genus; form as in Jedlicka's colored figure; *Brachinus*-like; head and prothorax yellow, elytra dark blue, lower surface posteriorly dark, legs yellow, antennae dark with 3 basal segments yellow; upper surface irregularly pubescent, front and pronotal disc

otherwise nearly smooth, elytra roughened. Length of New Guinean individual 5.3 mm.

Type. From **Java**, in British Mus. (seen).

Occurrence in New Guinea. **N-E. N. G.**: 1, Wareo, Finschhafen ("Finsch Haven") (Rev. L. Wagner, South Australian Mus.).

Notes. Specimens of *Omobrus* which may all be assignable to *praetextus* have now been found in **Java**, **Malaya**, the **Philippines** including Luzon (at Baguio, Darlington), **New Guinea**, and the **Solomons**. The Philippine form seems to be a (slightly defined) subspecies, *punctulatus* Jedlicka, and the Solomon Is. form has been described as subspecies *brachinoides* by Van Emden. The New Guinean form also may prove to be slightly differentiated, but I do not care to describe it on the basis of the single known specimen.

My Philippine specimens were found (near Baguio) under stones where the ground was damp with seepage, at altitudes of *c.* 2000 m.

Genus *PARENA* Motschulsky

Parena picea (Macleay)

Darlington 1968, Part III, p. 139.

Additional material. **N-E. N. G.**: 1, Markham R., 50 m, Jan. 20–25, 1962 (Sedlacek); 1, Mt. Otto summit, Nov. 1965 (Dept. Agr. Port Moresby).

Genus *DEMETRIDA* White

Darlington 1968, Part III, p. 140.

Notes. Besides the 3 new species described below and the specimens of a few previously described species recorded in detail, 177 additional New Guinean specimens of this genus have been received since Part III went to press. Some additional new species may be represented in this material, but their discrimination would require more extensive study than I can undertake now.

For *Demetrida* in the Moluccas, see Darlington, 1968a.

Demetrida nigripes Darlington

Darlington 1968, Part III, p. 171.

Additional material. **West N. G.**: 1, Waigeo Is., Mt. Nok, Camp 2 (Buffelhorn), June 1938 (Cheesman).

Notes. The two previously known specimens of this very distinct species were from localities in **Papua** and **N-E. N. G.** respectively. The present specimen extends the known range of the species to beyond the western tip of New Guinea.

Demetrida nigriceps Darlington

Darlington 1968, Part III, p. 174.

Additional material. **West N. G.**: 3, Wissel Lakes (Moanemani and Enarotadi), 1500, 1850, 1850–1900 m, dates in June, July, Aug., 1962 (Sedlacek). **N-E. N. G.**: 1, Mt. Missim, 1600–2000 m, Sept. 21–24, 1964 (M. Sedlacek).

Notes. The 2 types, from Sibil Valley, Star Mts., **West N. G.**, were both ♂♂. The 4 individuals recorded above are all ♀♀. They compare well with the types, but ♂♂ are necessary to confirm the identification.

Demetrida karimui n. sp.

Description. With characters of genus; rather slender, normally convex; head, prothorax, base and apex and (very narrowly) lateral margins of elytra black, disc of elytra broadly red, legs black, antennae and tarsi brown; reticulate microsculpture indistinct. *Head* 1.02 and 1.05 width prothorax; eyes prominent, genae very short. *Prothorax* subquadrate except angles rounded to neck in front; width/length 1.00 and 0.99; base/apex 1.43 and 1.54 (but apex can not be measured exactly); base/head 0.92 and 0.95; sides rather weakly rounded anteriorly, sinuate well before *c.* right but blunted basal angles; margins rather narrow, each with seta-bearing puncture slightly before middle but none at base; disc with deep entire middle line, other impressions very weak, surface slightly irregular or subpunctate baso-laterally. *Elytra*: width elytra/pro-

thorax 1.97 and 2.07; apices with short spines or very acute teeth, with outer angles right or acutely subdenticulate; striae slightly impressed, punctulate; intervals very slightly convex, 3rd 2-punctate. *Claws* with *c*. 5 teeth. *Secondary sexual characters* of ♂ unknown; ♀ with 4 or 5 apical ventral setae each side. *Measurements*: length 8.2–9.6 mm; width 2.8–3.2 mm.

Types. Holotype ♀ (Bishop Mus.) and 3 (all ♀♀) paratypes (2 in MCZ, Type No. 31871) all from Karimui, **N-E. N. G.**, 1080 m, July 13 (1 paratype July 14–15), 1963 (Sedlacek).

Notes. In my key to the New Guinean species of *Demetrida* (Part III, pp. 146ff), this runs to couplet 47, and falls with *saidor*. However, as compared with *saidor*, the present new species has a relatively narrower head and narrower elytra (compare proportions given) and differs in color, the elytra being entirely bordered with black (only humeri or small basal area black in *saidor*). The color recalls *D. dorsalis* (Part III, p. 171), but the latter has a much wider prothorax; the present species is probably not related to *dorsalis*. The present species also resembles *D. discoidalis* (Part III, p. 181) but lacks the posterior-lateral prothoracic setae of the latter, and has the elytra more extensively red; again there is probably no direct relationship between these two species. The general similarity of color of *D. dorsalis*, *discoidalis*, and *karimui* is probably simply convergent, or possibly mimetic.

Demetrida parena n. sp.

Description. With characters of genus; form as in Figure 80; black, elytra faintly greenish in some lights, appendages reddish brown; reticulate microsculpture isodiametric on front, faint and somewhat transverse on pronotum, more distinct and and much more transverse on elytra. *Head* 0.86 width prothorax; eyes large, prominent, with genae short and oblique. *Prothorax*: width/length 1.34; base/apex 1.49; base/head 1.05; sides rather strongly sinuate well before *c*. right slightly blunted posterior angles; margins moderate, not strongly reflexed, each with seta-bearing puncture at or slightly before middle but none at base; disc with middle line coarse and entire, transverse impressions very weak, surface subpunctate across base and in margins. *Elytra* short (in genus); width elytra/prothorax 1.81; outer angles obtuse but distinct, apices short-spined, sutural angles obtuse; striae moderately impressed, faintly punctulate; intervals very slightly convex, sparsely punctulate, 3rd 2-punctate. *Claws* with *c*. 4 teeth. *Secondary sexual characters*: ♂ unknown; ♀ with 3 or 4 (unsymmetric) seta-bearing punctures each side last ventral segment. *Measurements*: length 9.4 mm; width *c*. 4.0 mm.

Type. Holotype ♀ (British Mus.) from Waigeo Is., **West N. G.**, Camp Nok, 2500 ft. (*c*. 660 m), Apr. 1938 (Cheesman); the type is unique.

Notes. This new species is apparently close to *D. imitatrix* Darlington of New Guinea (1968, Part III, p. 176) but differs in color, being black with elytra at most faintly greenish (not blue) and with appendages reddish brown (not dark). It differs also slightly in proportions, especially in having a slightly broader prothoracic base than *imitatrix*.

In appearance, except for the spined elytra, this new species looks like an unmarked *Parena*, from which the specific name is derived.

Demetrida viridipennis Darlington

Darlington 1968, Part III, p. 177.

Additional material. **N-E. N. G.**: 1, Herzog Mts., Morobe Dist., Vagau, 4000 ft. (1220 m), Jan. 4–17, 1965 (Bacchus, British Mus.), Station No. 144. **West N. G.**: 1, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Notes. This species is known from a number of localities in **Papua** and **N-E. N. G**, but the Japen Is. specimen is the first recorded from **West N. G.**

Demetrida aiyura n. sp.

Description. With characters of genus; form *c.* as in *D. seticollis* (Part III, Fig. 109) but differing slightly in proportions (see following ratios), without extra pronotal setae, and with longer elytral spines; brown, head and prothorax castaneous, elytra paler except slightly darker near base and sides, appendages slightly paler; shining, reticulate microsculpture absent on front and pronotum and scarcely distinct (apparently *c.* isodiametric but very lightly impressed) on elytra. *Head* 1.10 and 1.13 width prothorax; eyes normally prominent, genae shorter, oblique. *Prothorax*: width/length 0.99 and 0.99; base/apex 1.42 and 1.31; base/head 0.92 and 0.90; lateral margins rather narrow anteriorly, slightly broader posteriorly, each with strong seta at basal angle, strong seta at or slightly before middle, but no trace of other anterior setae or formerly-seta-bearing punctures; disc with strongly impressed middle line, weak transverse impressions, surface slightly irregular but not punctate basally. *Elytra*: width elytra/prothorax 2.00 and 2.04; apices with outer angles acute but not much produced, long-spined *c.* opposite ends 3rd intervals, with sutural angles obtuse; striae slightly impressed, slightly punctulate; intervals slightly (scarcely) convex, 3rd 2-punctate. *Claws* with *c.* 5 teeth. *Secondary sexual characters*: ♂ tarsi as genus; ♂ middle tibiae slightly bent out, tuberculate-serrate in distal third of inner edge (*c.* 4 tubercles); ♂ with 3, ♀ 3 or 4 (unsymmetric) setae each side last ventral segment. *Measurements*: length 9.4–10.0 mm (including elytral spines); width 2.9–3.5 mm.

Types. Holotype ♂ (British Mus.) from Aiyura (nr. Kainantu, E Highlands), **N-E. N. G.**, (altitude probably *c.* 1500 m), Sept. 25, 1957 (J. Smart); 1 ♀ paratype (Bishop Mus.) from Pindiu, Huon Pen., **N-E. N. G.**, 870–1300 m, Apr. 21–22, 1963 (Sedlacek).

Notes. I hesitate to describe another species in this genus from 2 specimens from different localities, but the specimens are clean and in good condition, and they agree well in proportions and nonsexual details except that the ♀ has the prothorax a little less narrowed anteriorly, with better defined anterior angles (reflected in the ratio of prothoracic base/apex). These specimens have characters which suggest the existence of a distinct, possibly ancestral population in a group of *Demetrida* in which several related species are localized. The group in question includes nonpubescent forms with posterior-lateral prothoracic setae present and with elytra spined. They are placed at the end of my key to the New Guinean species of *Demetrida* (Part III, pp. 146–149), in couplets 57ff. From the species there named, the present new one is distinguished from *seticollis* by lacking extra anterior-marginal prothoracic setae, and from the others (*pallipes*, etc.) by brown color, the others being wholly or mainly black, blue-black, or greenish-black, and often with dark legs. Although the present new species is based on only 2 individuals from different localities, its immediate relatives (indicated above) are known from series which indicate that variation within single populations is not excessive.

If it were not for the presence of posterior-lateral prothoracic setae, this species would run (in the key referred to above) to *forma* (Part III, p. 167), which may be a composite species. However, *aiyura* differs from typical *forma* (the measured ♂ ♀) in proportions of base of prothorax/width of head and of width of elytra/prothorax, as well as in presence of the posterior prothoracic setae.

Tribe PENTAGONICINI

Genus *PENTAGONICA* Schmidt-Goebel

Darlington 1968, Part III, p. 192.

Notes. Nine additional New Guinean specimens seen.

Genus *SCOPODES* Erichson

Darlington 1968, Part III, p. 197.

Notes. Five additional New Guinean specimens seen.

Tribe HEXAGONIINI

Genus *HEXAGONIA* Kirby

Darlington 1968, Part III, p. 202.

Notes. The following new species, the second of the genus to be found in New Guinea, is not directly related to the other (*papua* Darlington, Part III, p. 203) but represents a different Oriental stock.

Hexagonia gressitti n. sp.

Description. With characters of genus; form as in Figure 81; brownish black, legs yellow, antennae dark brown; shining, reticulate microsculpture absent on front and pronotum and indistinct on elytra. *Head* 0.95 width prothorax; antennae short; mandibles long, nearly straight; front transversely grooved anteriorly, broadly impressed each side between eyes. *Prothorax* cordate; width/length 1.26; base/apex 1.29; lateral margins narrow but separated from disc by channels, each with seta-bearing puncture *c.* ⅓ from apex but none at base; disc with deep middle groove, other impressions subobsolete, impunctate. *Elytra*: width elytra/prothorax 1.43; striae impressed, punctate; intervals slightly convex, 3rd 3-punctate (1 near base on outer edge, 2 behind middle), 5th with 1 puncture on outer edge *c.* ⅓ from apex. *Lower surface*: sides of prosternum (but not most of proepisterna) with some coarse punctures; abdomen somewhat roughened. *Legs*: moderate; tarsi wide; 4th segments deeply emarginate; claws not toothed. *Secondary sexual characters*: ♂ front tarsi apparently without sexual squamules; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements*: length 6.0 mm; width 2.0 mm.

Type. Holotype ♂ (Bishop Mus.) from Nabire, S of Geelvink Bay, **West N. G.**, 1–20 m, July 8, 1962 (Gressitt); the type is unique.

Notes. This is much smaller than the single previously known New Guinean *Hexagonia* (see under genus), differently colored (not bicolored), and differently shaped. It has evidently been derived from the Orient independently. General form and plain brown color seem to relate it to several Oriental species including *bowringi* Schaum, but *gressitti* is distinct from all of them by its small size and relatively long, slender, nearly straight mandibles.

Tribe ODACANTHINI

Genus *DOBODURA* Darlington

Dobodura armata Darlington

Darlington 1968, Part III, p. 215.

Additional material. **N-E. N. G.**: 1, nr. Okapa, Wanatabe Vy., E Highlands, *c.* 5000 ft. (1525 m), Feb. 5, 1965 (Bacchus, British Mus.).

(Genus *ANDREWESIA* Liebke)

Liebke 1938, Festschrift Embrik Strand, 4: 84 (not *Andrewesius* Jedlicka 1932, Ent. Nachrichtenblatt, 6: 74).

(*Andrewesia apicalis* (Chaudoir))

Chaudoir 1872, Bull. Soc. Nat. Moscow, 45 (1): 408 (*Odacantha*).
Andrewes 1930, Cat. Indian Carabidae, p. 229 (*Odacantha*).
Csiki 1932, Coleop. Cat., Carabidae, Harpalinae, 8: 1536.
Liebke 1938, Festschrift Embrik Strand, 4: 85.
Louwerens 1967, Ent. Meddelelser, 35: 202.

Description. None needed here.

Types. From **Bangkok** and **Singapore**, presumably in Oberthür Coll., Paris Mus. (not seen).

Occurrence in New Guinea. Doubtful.

Notes. I did not refer to this species in Part III because I failed to note that New Guinea is included in its range by Csiki and (presumably following Csiki) by Louwerens. I have been unable to find the source of the New Guinean record. It may be a compiler's error. Or it may be based on a misidentified specimen of the species described by me (Part III, p. 214) as *Eudalia anomala.* There are taxonomic problems

here at both the generic and specific levels which I cannot solve now.

Tribe ZUPHIINI (LELEUPIDIINI)

Leleupidiini Basilewsky 1951, Revue Zool. Bot. Afr., 44: 178.
——— 1953, Revue Zool. Bot. Afr., 47: 264.
——— 1954, Revue Française d'Ent., 21: 213.
——— 1967, Bull. Soc. Ent. France, 72: 250.
Landin 1955, Arkiv f. Zoologi, ser. 2, 8: 467 (*Guncorita*, new genus from Sikkim, evidently a leleupidiine).

This group of small-eyed, flightless, antlike carabids differs from more ordinary Zuphiini in having the first antennal segment not scaphiform, the palpi remarkably modified, and in other details. Whether it should be recognized as a separate tribe or as a subgroup within the Zuphiini is a matter of point of view—of how many tribes one wishes to recognize within the family Carabidae. The leleupidiines are surely a distinct group worthy of at least subtribal recognition.

Most leleupidiines are African (and 1, Madagascan), but 2 have been described from southern Asia, and the range of the group is now extended to New Guinea. As Basilewsky (1954) suggests, the group is probably old (originally dispersed, I should think, by winged ancestors) and now has a relict distribution, the (flightless) survivors occurring on certain mountains in Africa and at scattered localities in southern Asia, etc.

Genus *COLASIDIA* Basilewsky

Basilewsky 1954, Revue Française d'Ent., 21: 215, fig. 1.

Type species. C. malayica Basilewsky, of Singapore.

Diagnosis (for identification in New Guinea only). Antlike Zuphiini; eyes small; first antennal segment not scaphiform; apical segment labial palpi greatly enlarged.

Description. None required here.

Generic distribution. At present known only from **Singapore** and **New Guinea**.

Notes. I am not prepared to discuss the relationships or differential characters of this genus in comparison with other leleupidiines.

The two New Guinean species described below (each known from a single ♀) resemble *malayica* (which also is known from a single ♀) in general but differ in details, especially in shape of the head and prothorax. These three species are all flightless now (unless they prove to be dimorphically winged), but their common ancestor that dispersed across the Malay Archipelago may have been winged.

Colasidia papua n. sp.

Description. With characters of genus; form as in Figure 82; brown, appendages paler; whole upper surface closely coarsely punctate and rather sparsely pubescent, but surface shining between punctures under the pubescence. *Head* 0.86 width prothorax; eyes moderate (large in group), enclosed behind by long genae; antennae moniliform, 1st segment scarcely longer than 3rd; mandibles short, transverse; labrum 6-setose; front almost evenly convex, with very small frontal impressions almost above antennal bases; 2 setae each side (doubtfully distinguishable from the general pubescence) over eye and at posterior corner of head; mentum with emarginate tooth at middle; labium subtruncate (slightly broadly emarginate), 1-setose each corner; paraglossae membranous, longer than labium. *Prothorax*: width/length 0.91; base/apex 1.32; posterior angles subbasal, dentiform; margins narrow, each with seta on dentiform posterior angle and *c.* ¼ from apex; disc strongly convex, scarcely impressed. *Elytra*: width elytra/prothorax 1.82; punctures not forming distinct striae, but intervals indistinctly indicated. *Inner wings* atrophied. *Lower surface* extensively punctate, but punctation absent on proepisterna and sparse on anterior-lateral portions of ventral segments. *Legs* moderately slender; tarsi rather long, segments not much lobed; claws simple. *Secondary sexual characters*: ♀ with 1 seta-bearing puncture each side

apex last ventral segment; ♂ unknown. *Measurements*: length 4.5 mm (to apex elytra) (*c.* 5.0 to apex abdomen); width 1.7 mm.

Type. Holotype ♀ (sex determined by dissection) (MCZ, Type No. 31875) from Dobodura, **Papua**, Mar.–July 1944 (Darlington); the type is unique.

Notes. This insect has a more oval head, more rounded posteriorly and with relatively larger eyes, than *Colasidia malayica* Basilewsky, and is probably much more coarsely punctate above. It is evidently endemic to New Guinea, and probably localized within the island. It cannot fly and therefore is unlikely to be taken in light traps. The type was taken struggling in flood water in rain forest, where a cloudburst had brought down a bank and blocked a small brook. The insect probably lives in or under leaf litter on the forest floor.

Colasidia madang n. sp.

Description. With characters of genus; form as in Figure 83; black, legs irregularly brownish, antennae brownish yellow; answering description of preceding species (*papua*) in detail (except mouthparts not examined) except as follows. Punctation of upper surface slightly finer and of head slightly less dense. *Head* 0.89 width prothorax; eyes smaller and more transverse than in *papua*. *Prothorax*: width/length 0.95; base/apex 1.40; posterior angles more prominent and more acute than in *papua*. *Elytra* slightly shorter and more rounded than in *papua*; width elytra/prothorax 2.07. *Measurements*: length 4.4 mm (to apex elytra) (5.0 to apex abdomen); width 1.75 mm.

Type. Holotype ♀ (sex determined by dissection) (British Mus.) from Damanti, Madang Dist., Finisterre Rge., **N-E. N. G.**, 3550 ft. (1083 m), "Stn. No. 34," Oct. 2–11, 1964 (M. E. Bacchus); the type is unique.

Notes. The differences between the two New Guinean species of *Colasidia* are indicated in the preceding description. The most important are that *madang*, as compared with *papua*, is black rather than brown, with smaller eyes, prothorax with more prominent and acute posterior angles, and slightly finer dorsal punctation. As compared with (the original figure of) *malayaca* Basilewsky, *madang* has the head less wide posteriorly, the prothorax with much more prominent and more acute posterior angles, and the whole upper surface probably more coarsely punctate.

Tribe HELLUONINI

Genus *HELLUONIDIUS* Chaudoir

Helluonidius latipes Darlington

Darlington 1968, Part III, p. 231.

Additional material. **N-E. N. G.**: 1, Finisterre Rge., Damanti, 3550 ft. (1083 m), Oct. 2–11, 1964 (Bacchus, British Mus.), Station No. 46; 1, Finisterre Rge., Budemu, *c.* 4000 ft. (1220 m), Oct. 15–24, 1964 (Bacchus, now in MCZ).

Notes. The Damanti individual is a ♂ with front tarsi with segments 2 and 3 narrowly 2-seriately squamulose; squamules are present also below segment 4 but may not be attached to it.

The unique type of *latipes* is from Rattan Camp, Snow Mts., **West N. G.**

Genus *HELLUOPAPUA* Darlington

Darlington 1968, Part III, p. 232.

Diagnosis (*revised*). Characters as given (1968) except ♂ front tarsi *either* without squamules *or* with 2 rows of minute squamules at middle of segments 2 and 3.

Generic distribution (*revised*). **West N. G.**: now known from the type species from Rattan Camp, Snow Mts., and from the following new species from Waigeo Is.

Notes. See *Notes* under the following species for discussion of this genus in relation to *Helluonidius*.

Helluopapua cheesmani n. sp.

Description. With characters of genus; form as in Figure 84; black, appendages

slightly brownish; shining, reticulate microsculpture absent or indistinct even on elytra. *Head* 0.89 and 0.93 width prothorax; genae rounded, slightly prominent; clypeus slightly sinuate-truncate, broadly triangularly produced at middle (slightly more than in *papua*), with several long setae each side but none near middle; front weakly convex, longitudinally impressed each side and transversely impressed anteriorly, sparsely irregularly punctate; mentum with acute triangular tooth and long pointed side lobes; ligula *c.* as in *papua* (but see *Notes* below). *Prothorax*: width length 1.39 and 1.43; base apex 0.75 and 0.72; base/head 0.66 and 0.61; lateral margins narrow, not interrupted; disc weakly convex, middle line and anterior transverse impression distinct, baso-lateral impressions small and weak, surface of disc irregularly coarsely punctate with impunctate areas each side of middle. *Elytra*: width elytra prothorax 1.35 and 1.34; striae deep, impunctate; intervals convex, each with a row of punctures each side. *Measurements*: length *c.* 23.0 mm; width 6.0 mm.

Types. Holotype ♂ (British Mus.) and 1 ♀ paratype (MCZ, Type No. 31877) both from Waigeo Is., **West N. G.**, Mt. Nok, Camp 2 (Buffelhorn), June 1938 (Cheesman).

Notes. I have been able to compare these specimens directly with the unique ♂ type of *Helluopapua toxopei* (which has not yet been returned to the Leiden Museum). The two species agree well in most generic characters including form of labrum, form of inner lobe of maxillae (but see below), and slender tarsi. However, while the ♂ of *H. toxopei* completely lacks sexual squamae on the front tarsi, that of *cheesmani* has minute white scales, in two series, on segments 2 and 3 only. In addition to this, the present new species differs from *toxopei* in having the elytra without distinct microsculpture, and in having the elytra relatively narrower (or the head and prothorax wider).

The hook of the inner lobe of the maxillae is more nearly apical in the present species than in *toxopei*, but still less strictly apical than in *Helluonidius.* The difference is actually due to the form of the outer apical angle of the maxillary lobe, which is considerably produced in *Helluopapua toxopei*, somewhat produced in the present new species, and not produced in *Helluonidius.*

The next reviser of this group will have to decide whether, in view of the fact that the present new species is in some way transitional between *Helluonidius* and *Helluopapua* (although much closer to the latter), the two genera should be kept separate.

Tribe BRACHININI

Genus *BRACHINUS* Weber

Brachinus papua Darlington

Darlington 1968, Part III, p. 239.

Additional material. **N-E. N. G.**: 1, Maprik (Sepik Dist.), Oct. 26, 1957 (J. Smart, British Mus.).

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IN LIEU OF INDEX

I had planned to add here an index covering all four parts of *The Carabid Beetles of New Guinea*, but have decided against it. To make the index would be very time-consuming; to print it would add materially to the cost of publication; and it would probably be of only limited use. In lieu of an index, therefore, I offer the following suggestions to users of this work.

The work should be arranged as suggested in the footnote on the first page of Part IV. The table of contents of Part IV will then come first, and will serve as a guide to the introduction and discussion of Part IV, which include references to important items in the shorter introductions of the other parts. Parts I, II, and III will come next, and cover the Carabidae of New Guinea in taxonomic order. Each of these parts has a table of contents which lists the tribes and genera treated, and the order is, of course, that of the *Coleopterorum Catalogus* (see Part IV, [4]), which all persons working seriously on Carabidae of remote parts of the world must have. The *Catalogus* will serve as an indirect index or at least a guide to the taxonomic part of the present work. And the *Zoological Record* indexes the new species. The taxonomic supplement of Part IV, placed last, also follows the order of the *Coleopterorum Catalogus*. I suggest that users of my work make marginal notes in Parts I to III indicating the genera and species treated in this supplement.

Bulletin OF THE
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A New Rhinoceros from the Late Miocene of Loperot, Turkana District, Kenya

D. A. HOOIJER

HARVARD UNIVERSITY [illegible]
CAMBRIDGE, MASSACHUSETTS [illegible]

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A NEW RHINOCEROS FROM THE LATE MIOCENE OF LOPEROT, TURKANA DISTRICT, KENYA

D. A. HOOIJER[1]

CONTENTS

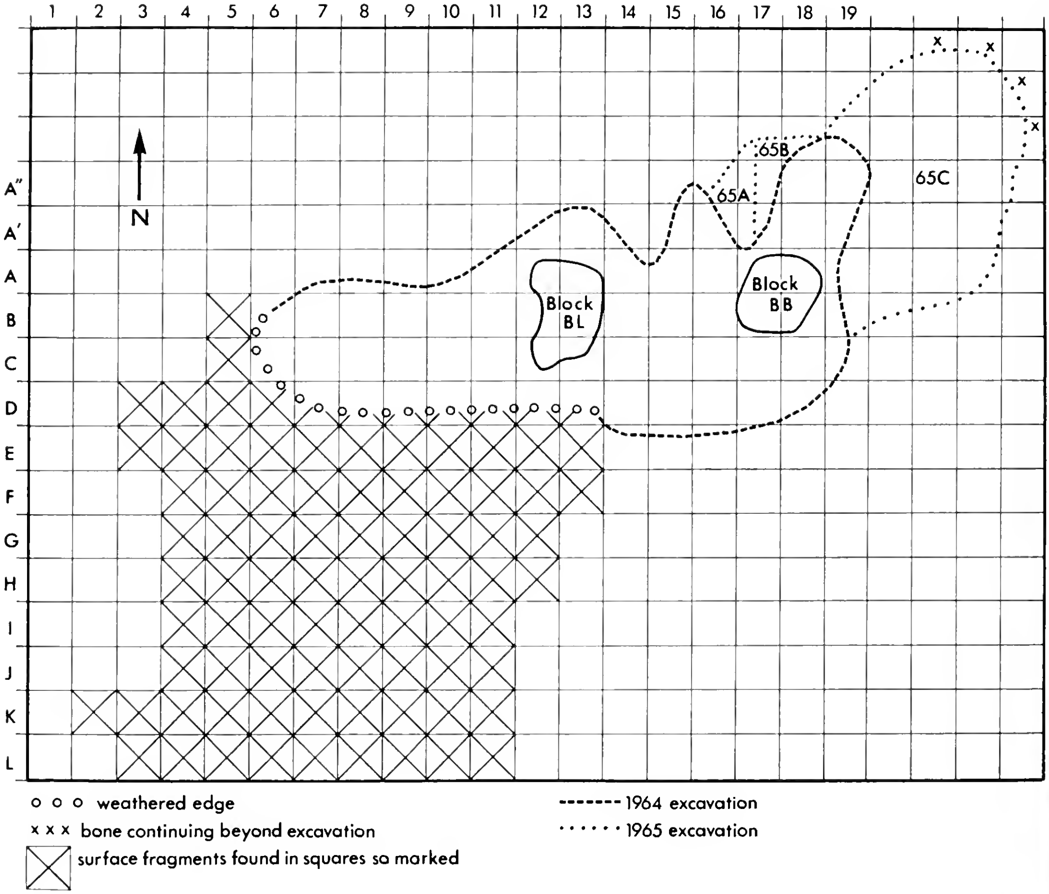
ABSTRACT. *Chilotheridium pattersoni*, a new genus and species of Rhinocerotidae from the late Miocene, Vindobonian, Turkana Grit Formation of northwestern Kenya, is described and compared with its close relatives *Chilotherium* and *Diceratherium*. The species also occurs at Ngorora. Fragments of *Chilotheridium* sp. from Bukwa II, Rusinga and Kirimun, of *Aceratherium* sp. or *Dicerorhinus* sp. from Kirimun and Ngorora, and of *Brachypotherium* sp. from Ngorora are recorded. Phalanges of a hippopotamid were mingled with the rhinoceros remains from the Turkana Grit; these constitute the earliest record of the family.

INTRODUCTION AND ACKNOWLEDGMENTS

In a paper on Miocene rhinoceroses of East Africa (Hooijer, 1966), a single last upper molar from the Turkana Grit Formation near Loperot, Turkana District, Kenya, collected in 1948 and preserved in the National Museum Centre for Prehistory and Palaeontology in Nairobi, was referred to the genus *Chilotherium* Ringström. To the same genus, and likewise without specific allocation, I referred two incomplete upper molars from Gumba and Wakondu on Rusinga Island. Teeth indistinguishable from those of *Chilotherium* have since been found at Bukwa II, Uganda (Walker, 1968), and at Ngorora, Kenya (collected by Dr. W. W. Bishop in 1968), early Miocene and early Pliocene, respectively. The Loperot rhinoceros has been cited as *Chilotherium* sp. by Leakey (1967: 15) and by Maglio (1969: 2).

In the years 1964 and 1965 Professor Bryan Patterson led field parties of the Harvard Museum of Comparative Zoology to the Loperot area, which is at latitude 02° 20′ N, and longitude 35° 50′ E, or 50 miles SSE of Lodwar and 45 miles SW of Lake Rudolf. The rhinoceroses collected were generously offered to me for description. The Loperot area has been geologically mapped by Joubert (1966), and three Potassium Argon dates are available for the lava overlying the fossil-bearing Turkana Grit, 17.5 ± 0.9 m.y. for a sample five feet above the contact with the Turkana Grit at the rhinoceros quarry, 16.7 ± 0.8 m.y. for a sample approximately 200 feet above the contact with the Turkana Grit in the Auwerwer Hills, and 15.8 ± 1.2 m.y. from a basalt boulder in the Turkana Grit at the base of the Auwerwer

[1] Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.



Text-figure 1. Map of the *Chilotheridium pattersoni* quarry, 70–64 K. The squares measure two feet to a side. Redrawn from expedition field notes.

Hills, 40 feet below the contact with the lava (Patterson, personal communication). The fossil-bearing beds at Loperot may be taken as early Vindobonian, late Miocene. They are older than those at Fort Ternan (*ca.* 14 m.y.). The rhinoceros of Fort Ternan, *Paradiceros mukirii* Hooijer (1968b), is widely different from that of Loperot in being bicorn, without lower canines, and with brachyodont cheek teeth, but its metapodials, so far as available, show a remarkable resemblance to those from the Loperot locality, as will be remarked upon in the proper places in the present monograph. A new genus and species of rhinoceros should ideally be based on skulls and teeth, as well as bones: I think we have such an ideal situation with the Loperot collection of Harvard. Rhinoceros remains make up the great bulk of the material collected from the Turkana Grit by the museum expeditions. All of them were found at the same level in the formation and in essentially the same spot. This locality is three and one-eighth miles north of the Kamuthia waterhole near the head of a dry wash known as Laminkwais (see map in Joubert, 1966), and the level is 55 feet below the overlying basalts of the Tvb_1 series. The great majority of the

rhinoceros remains come from one quarry in a bed of light brownish pink, jointed mudstone, in which the other specimens were also found. The state of preservation is poor: most of the teeth and bones are crushed and broken and the broken surfaces are not clean and sharp, being abraded as a result of postdepositional movements in the sediment. Nearly all of them were entirely dissociated and piled against or upon each other. The one exception is a right pes from the quarry, which is represented by most of its elements. Remains of at least twelve (and probably many more) individuals are represented, eight of them in the quarry. This mass occurrence with very little in the way of other animals is reminiscent of conditions at the famous Agate Springs *Diceratherium* quarry in the Miocene of Nebraska. Numbers of rhinoceroses evidently perished at these localities, perhaps along the courses of streams and rivers that were drying up during a prolonged dry season, the bones being subsequently swept by floods into a catchment area. Professor Patterson informs me that the *Chilotheridium* quarry was not exhausted when excavation of it was stopped in 1965. Parties working the area in the future should be able to collect additional material there.

The associated fauna of the Turkana Grit has as yet been mentioned only in part. Maglio (1969) records a tusk fragment of a shovel-tusked gomphothere, a very early member of the group, which suggests that Africa may have been the continent of origin of the amebelodontines. A similar conclusion may be drawn as to the hippopotamids: serendipitously, during the study of the Loperot collection it was found that there are a number of phalanges in 68–64K and 70–64K not or hardly distinguishable from those of the modern *Hippopotamus amphibius*. As the oldest remains of hippopotamids known to date are from the early Pliocene (Pontian) of Sicily and Spain (Hooijer, 1946; Aguirre, 1963), the Loperot hippopotamus is the earliest in the world. Maglio (1969) cites as elements of the Loperot fauna *Deinotherium hobleyi* Andrews, *Chilotherium* sp. (now *Chilotheridium*), *Brachyodus* (?) sp., *Dorcatherium* cf. *pigotti* Whitworth, and a hyracoid aff. *Prohyrax*.

As I was studying the collection, it became increasingly evident that the cranial and postcranial skeletal remains of this rhinoceros differed rather markedly from those of the genus *Chilotherium*, no matter how closely the dentition resembled that of this genus. In fact, had cranial and postcranial material not been found in association with the teeth, the East African form of rhinoceros described in the present paper would still have been called *Chilotherium*. As the material other than dental cannot be placed in any genus of rhinoceroses at present known, the Loperot rhinoceros is here referred to a new genus and species, *Chilotheridium pattersoni* gen. et sp. nov.

It has been necessary to use the original field numbers in this paper. Thus, 68–64K means the sixty-eighth specimen or lot collected in Kenya by the 1964 expedition of the museum. The quarry bears the collective number 70–64K and combinations following this number, such as BB and A17, denote the position of a bone in the quarry (see Fig. 1). In addition, the various elements, skull, mandible, scapula, humerus, etc., have been consecutively numbered for each kind. All specimens are the property of the National Museum of Kenya and will in due course receive the permanent catalogue numbers of that institution.

I am greatly indebted to Professor Bryan Patterson for offering me the Loperot rhinoceros remains for study and report. I am likewise grateful to Dr. L. S. B. Leakey for allowing me to describe the Kirimun tusk of *Chilotheridium*, to Dr. W. W. Bishop for permission to record the Ngorora *Chilotheridium*, and to Dr. Alan Walker for sending me casts and data on the Bukwa II *Chilotheridium*. Professor Patterson's field work was supported by

National Science Foundation Grant No. G.P. 1188.

Family *Rhinocerotidae* Owen, 1845
Chilotheridium gen. nov.

Diagnosis. Small single nasal horn in both sexes; premaxillaries weak, no upper I; frontals and parietals pneumatized; orbit not placed so near upper contour of skull as in *Chilotherium*; cranium and occiput rather narrow; parietal crests not widely separated; inferior squamosal processes not united below; symphysial portion of mandible narrow, slightly expanding anteriorly. Cheek teeth fully hypsodont as in *Chilotherium* and with the same pattern: uppers with paracone style fading away basally and posterior portion of ectoloph flattened; protocone well set off by folds and flattened internally; anterior fold in metaloph, marking off hypocone; antecrochet prominent basally, curving inward to medisinus entrance; crochet usually well developed, and crista weak or absent; metacone bulge at base in M^3; anterior cingulum strong, internal cingulum weak and usually forming cusp at medisinus entrance. Lower canine subtriangular in cross section, depressed dorsoventrally, internal edge sharpened by wear, outer lower edge rounded, and outer upper edge ridged. Scapula low and wide; limb and foot bones not much shortened; radius and ulna, and tibia and fibula not ankylosed; radius with cuneiform facet; lunar without facet for ulna; metacarpal V present, three-fifths the length of metacarpal IV; lateral metapodials somewhat divergent posteriorly; femur with small third trochanter; calcaneum without tibia facet; navicular nearly rectangular; cuboid wider than high; metatarsal III with small cuboid facet.

Type species. Chilotheridium pattersoni sp. nov.

Chilotheridium pattersoni sp. nov.

Diagnosis. As for the genus.

Type. Skull No. 2 described and figured in the present paper (70–64K, B12).

Hypodigm. The type and numerous other elements (see Appendix, p. 390).

Horizon and locality. Turkana Grit; vicinity of Loperot, Turkana district, Kenya.

Age. Late Miocene, Vindobonian.

Name. The specific name is given in honor of Professor Bryan Patterson, who let me have the Loperot material for study.

SKULL AND DENTITION OF *CHILOTHERIDIUM PATTERSONI* GEN. ET SP. NOV.

Two skulls from the Loperot rhinoceros quarry, with most of the dentition, establish the uniqueness of the rhinoceros from this site; they will be described in the following pages.

Loperot skull No. 1 (70–64K, C9–10), four views of which are given, (Pl. 2, figs. 1–3, Pl. 3, fig. 1) is a much deformed specimen that is broken into innumerable small pieces. Plaster has been applied wherever needed to hold the skull parts together, evidently in the position in which they were found. Most of the right side of the skull is concealed by a thick mass of plaster, exposing only part of the occiput (both occipital condyles are there, but too close together and displaced to the right of the median line of the skull), part of the temporal fossa, the nasal, and the premolars and molars, which lack their outer portions. Of the skull base we find the body of the sphenoid embedded in plaster and lying obliquely to the right.

The left side of skull No. 1 is better preserved; it is, however, much depressed because of crushing in the middle, and the top of the occiput is missing. The fronto-parietal crest does not meet its fellow on the right side but remains a few centimeters distant from it. The postglenoid process is heavy, and does not unite with the posttympanic process below the external auditory meatus. The glenoid cavity is partially restored with plaster. The zygomatic arch is pressed downward and has been restored from fragments that do not

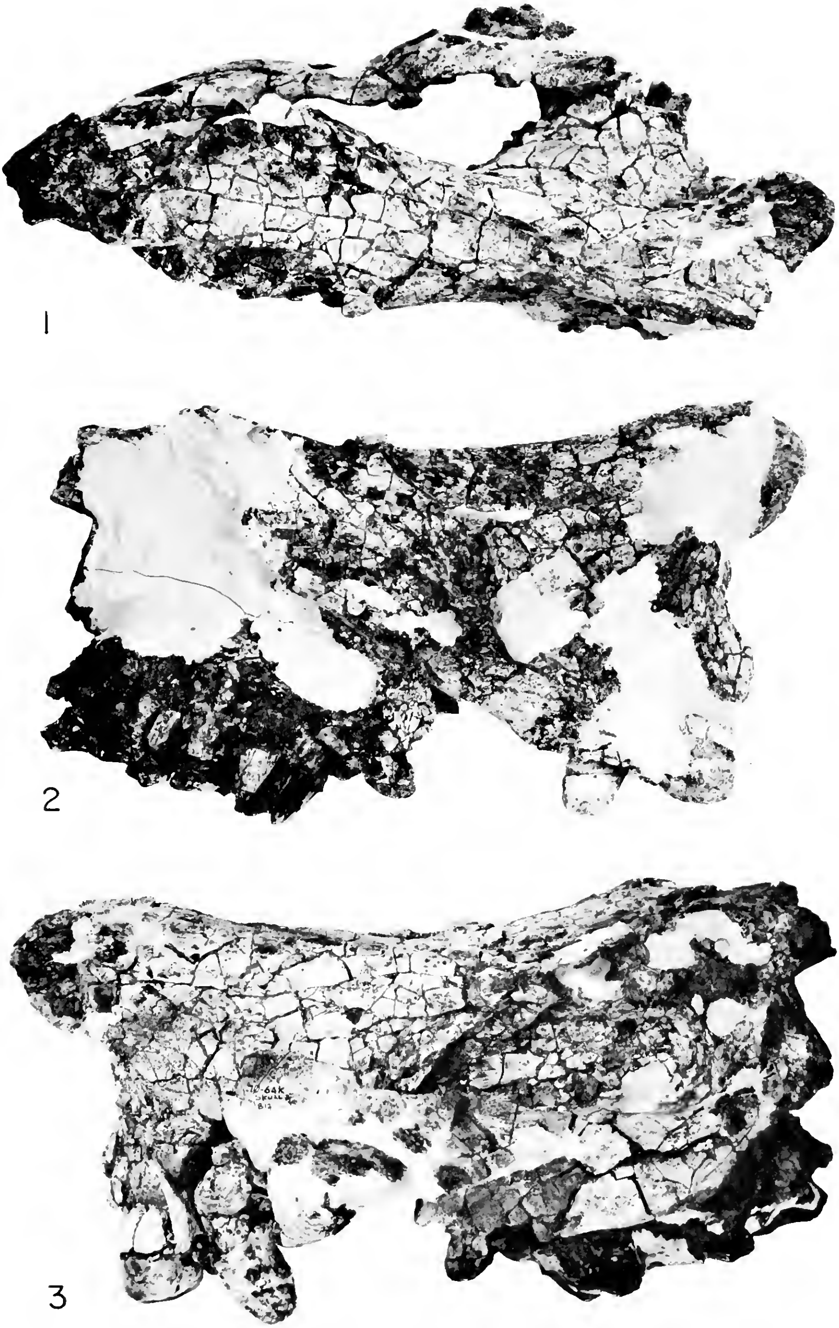


Plate 1. *Chilotheridium pattersoni.* Skull No. 2 (70–64K, B12), type. Fig. 1, top view; fig. 2, left view; fig. 3, right view. × 0.25.

fit very well. The orbitotemporal fossa is so crushed that the position of the orbit cannot be made out. Because of crushing, the anterior frontonasal region of the skull lies much higher than the middle part of the skull, and holds most of the nasals, which show a rugose area for a horn. The nasals, about 55 mm wide and only 25 mm high at a point about 10 cm in front of the nasomaxillary notch, suddenly expand vertically to a height of 43 mm, where there begins a rugose horn boss 60 mm long and 35 mm wide, with a weak median groove. The nasals diminish to a width of 48 mm and a height of 30 mm at the front end of the horn boss, and are broken off 1 cm in front of the boss. The ventral surface of the nasal bones is flat (Pl. 5, figs. 1–2).

The depth of the nasomaxillary notch is considerable (the portion of bone embedded in the plaster above the P^2 on the left side does not belong there). As seen on the right side the nasals are free for about 10 cm behind the horn boss, that is, to above the P^4–M^1 junction.

The dentition of skull No. 1, at least that on the left side, is rather well preserved, considering the state of preservation of the cranium. The right toothrow lacks P^2 and M^3 entirely and the outer parts of P^3–M^2. The inner columns of these teeth are nearly all broken.

P^2 is worn to a height of 17 mm from the crown base externally, and has medisinus as well as postsinus closed off as fossettes. The entrance to the medisinus forms an indentation. There is a very weak internal cingulum. The ectoloph is regularly convex with no styles showing.

P^3, the worn crown of which is 28 mm high externally, has the same two fossettes, and a trace of a cingulum at the base of the internal indentation representing the entrance to the medisinus. On the ectoloph there is only one style, the paracone style, more distinct above than at the base of the crown.

P^4, 45 mm high externally, as worn, has the antecrochet touching the metaloph, just about to close off the medisinus, in which a weak crista and a bifurcated crochet are seen. The postsinus is still open behind as the level of the posterior cingulum has not yet been reached by wear. The internal cingulum is manifest as a weak ridge along the bases of proto- and metaloph, and at the medisinus entrance. On the ectoloph, the paracone style, again, is seen to flatten out basally, while there is no metacone style. At this stage of wear, the anterior and posterior protocone folds, and the anterior hypocone fold, can be seen distinctly.

M^1, about 40 mm high as worn at the ectoloph (part of it is plaster), is not very well preserved: most of the metaloph is missing. The crochet, however, is there; it is well developed but does not block the medisinus. In the protoloph, the constriction of the protocone is very marked, and the antecrochet can be seen distinctly. The internal cingulum is barely indicated.

M^2, worn externally to a height of 60 mm, has the metaloph displaced upward and forward, making the medisinus too narrow. It has the same characters as M^1, but shows in addition that the paracone style disappears in the basal part of the crown, which is depressed only between the roots.

M^3 is unfortunately broken at the junction of proto- and ectoloph; the protoloph is displaced somewhat inward, with the cleft filled with plaster, so that the anterotransverse diameter cannot be given. The top of the ecto-metaloph (outer surface) internal to the large crochet is broken off. The crown is worn to a height of 70 mm, and there has not been very much wear, as seen from the narrow worn edges of the lophs. The unworn crown of M^3 would not have been more than some 5–10 mm higher. As the basal length of the outer surface is 62 mm, this is a decidedly hypsodont crown. At 50 mm above the base the length of the outer surface still amounts to 52 mm.

The M^3 of "*Chilotherium* spec." from Loperot described earlier (Hooijer, 1966:

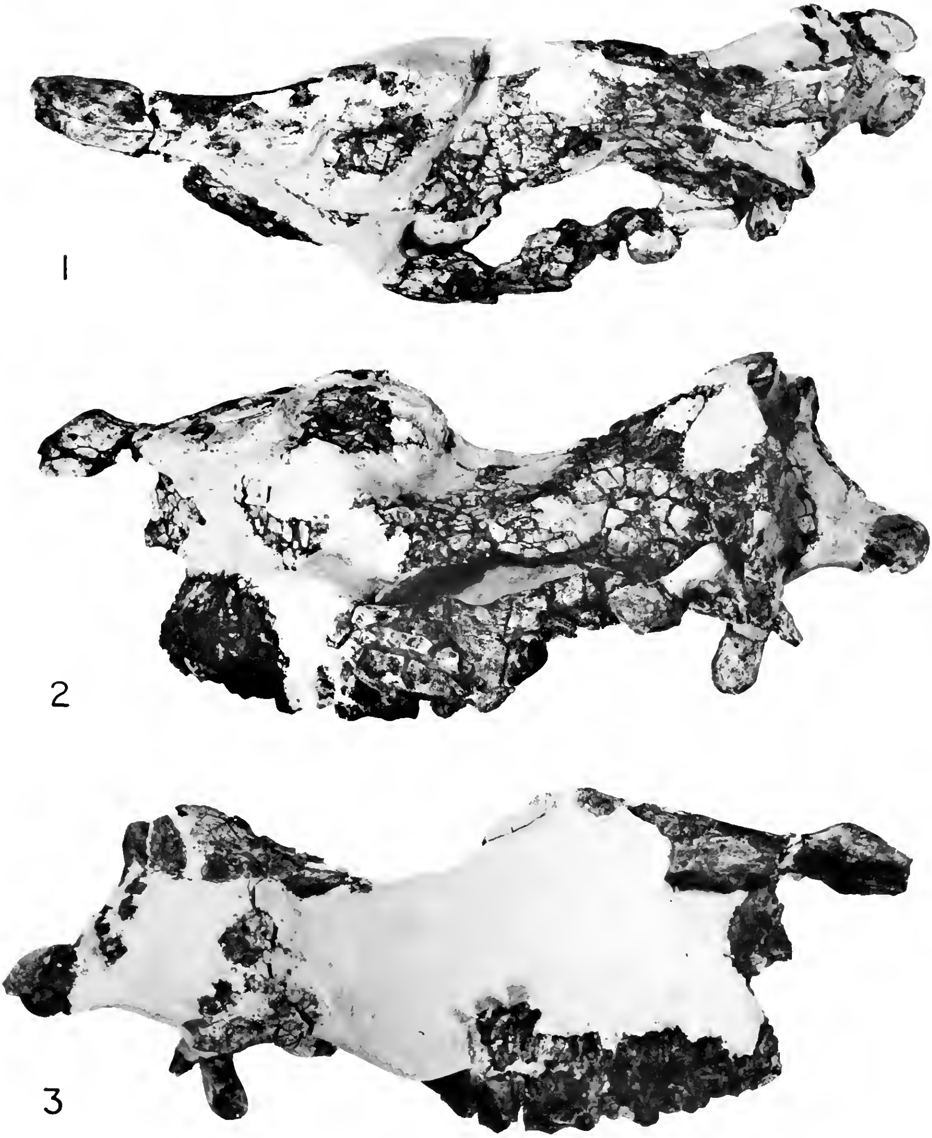


Plate 2. *Chilotheridium pattersoni*. Skull No. 1 (70-64K, C9-10). Fig. 1, top view; fig. 2, left view; fig. 3, right view. × 0.17.

150–152) is only a trifle smaller, and more worn, but resembles that in skull No. 1 very closely indeed. The paracone style, fading away basally; the internally flattened, constricted protocone; the basally prominent antecrochet (the medisinus base is broken and filled with plaster); the metacone bulging out basally; and, the posterior cingulum forming a point some 20 mm high, are all very much as in the 1948 Loperot specimen.

Loperot skull No. 2 (70–64K, B12) is better preserved than skull No. 1, and is the holotype of *Chilotheridium pattersoni* gen. et sp. nov. Four views of the specimen are given (Pl. 1, figs. 1–3; Pl. 3, fig. 2). Although this specimen, too, is broken into numerous small fragments held together by matrix, plastic, or plaster, there is not as much distortion. Most of the right side of the skull is there; the nasals and the premolar-bearing part of the palate are broken off but are preserved separately. On the left side the palate, zygomatic arch and occiput are missing, and the temporal fossa is pushed inward. This side of the skull is much fortified with plaster.

Seen from the right side, then (Pl. 1, fig. 3), the dorsal surface of skull No. 2 is weakly concave anteroposteriorly and flat transversely, with no trace of a horn boss on the frontals. The postorbital processes of the frontals are damaged, but the width over these can be given approximately. The two frontoparietal crests converge behind the orbit to a least distance of 25 mm, and then diverge into the temporal crests, of which only that on the right side is preserved. The occiput is notched in the median line above, and projects backward slightly beyond the occipital condyle. The occipital surface, of which only the right half (without the paroccipital process) remains, has been restored with plaster just above the beginning of the depression for the nuchal ligament. The zygomatic arch bears a slight postorbital process, behind which it is heavily restored with plaster. As it is, the arch is much extended along the fractures, and it ends below the glenoid cavity, which is distorted, too. The postglenoid process is, however, well preserved, and does not unite with the posttympanic process but remains a few millimeters distant from it below the external auditory meatus. The anterior border of the orbit is placed above the anterior border of M^2. Because of superficial damage the infraorbital foramina cannot be located. The nasomaxillary notch extends backward to above the anterior border of M^1. The nasals have broken off a few centimeters from the deepest point of the notch. Fortunately, however, there were many fragments of the nasal bones, and it has been possible to restore them; although they do not fit on to the skull, they doubtless belong to the same individual.

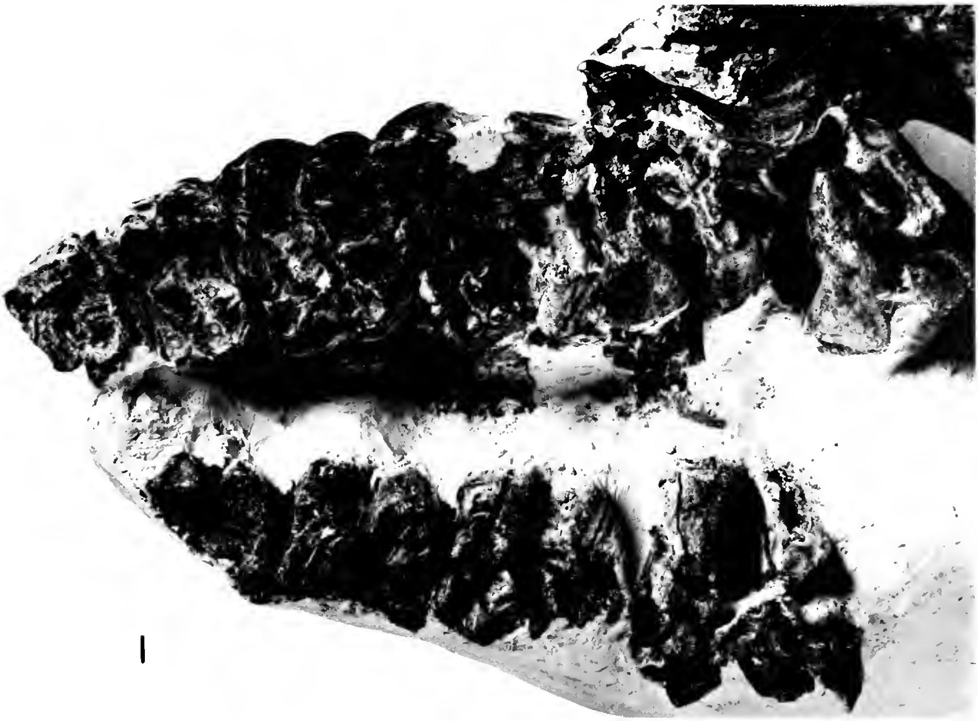
The portion of the nasals preserved (Pl. 4, figs. 2–3) is 14 cm long, and shows the weak median horn boss, 55 mm long and 35 mm wide, grooved in the middle. The height of the nasals from the top of the boss is 42 mm behind, and over 30 mm in front. Anterior to the horn boss the nasals form a projection about 45 mm long and 33 mm wide, bluntly pointed.

The premolars (in the maxillary portion: Pl. 4, fig. 1) and the molars are more worn than those in skull No. 1. Whether or not there was a persistent DM^1 cannot be made out in this specimen. Very little is preserved of the premaxillaries, which seem rather weak and were in all probability edentulous.

P^2, worn down to 8 mm from the crown base, shows only two small enamel pits of the medisinus and the postsinus, and a weak internal cingulum.

P^3 shows the same two pits, and an inner cingulum forming a point at the indentation representing the entrance to the medisinus. Its crown is worn down to 15 mm from the base.

In P^4, of which the outer portion is missing, the crown is still 20 mm high internally. The deep grooves delimiting the protocone (which is split vertically, the cleft being



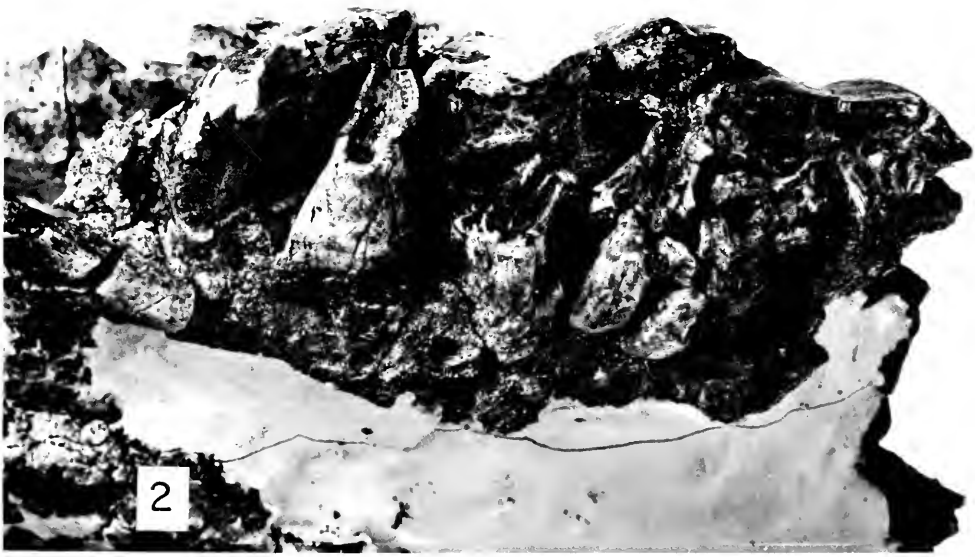


Plate 3. *Chilotheridium pattersoni*. Fig. 1, LP^2–M^3, RP^2–M^2 of skull No. 1 (70–64K, C9–10), crown view. × 0.50. Fig. 2, RM^1 (part)–RM^3 of skull No. 2 (70–64K, B12), type, crown view. × 0.70.

filled with matrix) are well shown, as is also the antecrochet next to it, which extends across the medisinus and joins the metaloph, cutting off the medisinus as a fossette. There is no trace of a crista or a crochet. The postsinus is closed off, too. The inner cingulum is continuous and well developed; it forms a conspicuous ridge at the medisinus entrance.

There is an anterior-internal fragment of the M^1 attached to the maxillary portion, showing neatly the anterior protocone fold. This portion belongs to the M^1 in the skull, but it cannot be replaced because of distortion of the bone. M^1, the outer surface of which is restored with plaster, is poorly preserved, having the metaloph with the crochet broken and distorted.

In M^2 the ectoloph (height as worn *ca.* 40 mm) is broken. Its structure is well shown: the strong antecrochet, the constricted protocone (split again, as in P^4), as well as the crochet, which extends forward externally of the antecrochet. There is no crista. The paracone style is weak, and fades out in the basal portion of the crown. The internal cingulum is continuous. There is an anterior fold in the metaloph opposite the protocone.

M^3, worn to 55 mm above the base, has the portion of the outer surface internal to the crochet broken and displaced, so that the length of the outer surface cannot be given. The protocone is flattened internally and well marked off by folds; the antecrochet is prominent basally and curves inward to the medisinus entrance. The outer surface is flattened especially toward the base, where the paracone style fades away. The metacone forms a bulge at the base, near the internal angle. The internal cingulum is present along the protocone, and, as a prominent cusp, at the medisinus entrance; it joins the posterior cingulum, which forms a point 28 mm high.

Apart from the more developed cingula and the absence of a (weak) crista in all the teeth, there is no difference between the dentition of skull No. 2 and that of skull No. 1.

There is further in the Loperot collection a right maxillary holding DM^1, P^{2-3}, DM^4 and M^1 (70–64K, 65B), representing a third individual (Pl. 7, fig. 3). The anteriormost tooth in this specimen is small, much worn down, and subtriangular, evidently a persisting anterior milk molar, DM^1. Its dimensions are *ca.* 25 mm anteroposteriorly, and *ca.* 20 mm transversely. In the middle of its broken worn surface it shows the base of the medisinus.

P^2 is broken, and the anterior part of its ectoloph is displaced forward, flanking the crown of the DM^1. It is 33 mm high externally, and not much worn; the protocone constriction can be seen clearly, but the metaloph (in part restored with plaster) is badly preserved.

P^3 is 42 mm high at the worn ectoloph, which is split vertically in the middle and distended along the fracture. A very small crista and a crochet are present, and the protocone constriction is very marked. The anterotransverse diameter of P^3 is 41 mm (less than that in skulls 1 and 2: Table 2), and the posterior width cannot be taken, as the metaloph is incomplete internally.

DM^4, the last milk molar, is rather worn but not broken: its greatest crown height is 25 mm. It shows all the characters of the first and second molars in skulls Nos. 1 and 2: the prominent antecrochet external to the constricted protocone, the anterior metaloph fold, the well-developed crochet, a trace of a crista, and the weak inner cingulum. The enamel is, of course, thinner, and the size less (anterotransverse 49 mm, posterotransverse 46 mm).

M^1 in the maxillary fragment is broken and incomplete internally. The external height of the worn crown is just about 60 mm.

The left maxillary belonging to the same individual as the right (70–64K, 65B) has a broken P^3, a DM^4 the ectoloph of which is displaced anteriorly but which is other-

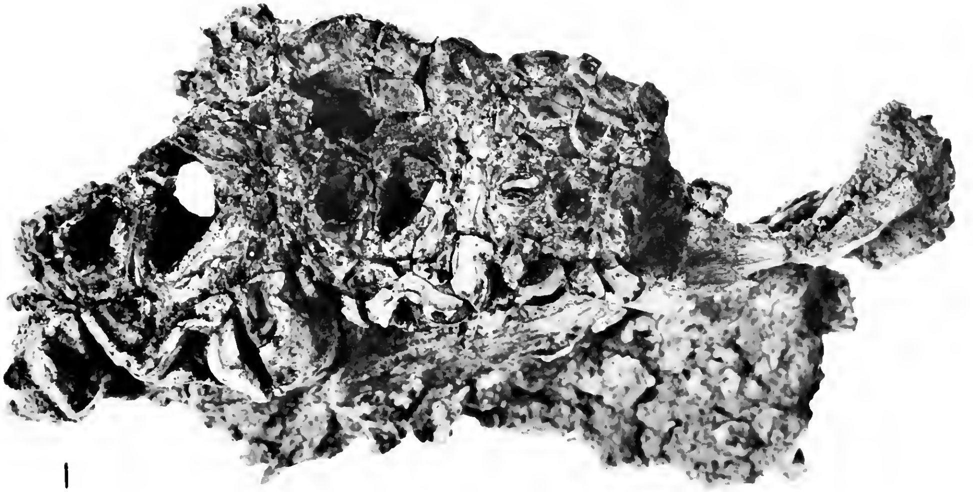


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Plate 4. *Chilatheridium pattersoni*. Fig. 1, RP^2–M^1 (part) of skull No. 2 (70–64K, B12), type, crown view. × 0.80. Figs. 2–3, nasals of same skull in right and top views. × 0.70.

TABLE 1. Measurements of the skull from Loperot (in mm)

	Loperot No. 2	*Chilotherium* China (Ringström, 1924)
Greatest length from occipital to tip of nasals	*ca.* 520	*ca.* 445–*ca.* 520
From occipital crest to front of orbit	360	290–322
Least distance between parietal crests	25	45–63
Width over postorbital processes of frontals	*ca.* 125	129–169
Distance from nasal notch to front of orbit	65	65–78
Width of nasals at 3 cm from tip	32	35–52
Height of occiput from lower border of foramen magnum	*ca.* 190	160–*ca.* 205
Greatest width of upper portion of occiput	*ca.* 115	*ca.* 135–175

wise a mirror image of RDM^4, and M$^{1-2}$ both transversely compressed. The M^2 is unworn and the ectoloph height of this molar is exactly 71 mm by a greatest anteroposterior ectoloph length of 62 mm, demonstrating the marked hypsodonty of the Loperot form.

Among the surface finds at 70–64K, C9–10, there are a number of tooth fragments making up a considerable part of an RM^3, similar to those described above. Its worn ectoloph is 63 mm high.

There is also a nasal portion in 70–64K, A″ 18, very much like those of skulls Nos. 1 and 2. The height of the nasals at the highest (posterior) portion of the horn boss is 52 mm, and the basal width at that level is 51 mm. The boss is shorter and wider than the others: length 50 mm, and width 38 mm. In front of it the nasals are only 34 mm high and wide; they taper to their blunt tip for a length of about 50 mm (Pl. 5, figs. 3–4).

Now that we have the skull as well as the upper dentition of the Loperot rhinoceros, it is easy to see that this form cannot be referred to *Chilotherium* as defined by Ringström (1924). *Chilotherium* has hornless, straight nasals, frontals and parietals not pneumatized, and the orbit placed just below the upper contour of the skull. The Loperot form, as we have seen, has a single, weak nasal horn boss, and the nasals are straight only as far as the ventral surface is concerned. The frontals and parietals are pneumatized: many air cells are seen on the broken surfaces. In keeping with this condition, found in most rhinoceroses except in *Teleoceras*, the orbit is not placed as high in the Loperot rhinoceros as in *Chilotherium*. As far as the hornlessness of *Chilotherium* is concerned, Bohlin (1937: 92) points to an indistinct, rugose structure on the nasal tips of a skull of *Chilotherium habereri* var. *laticeps* from Shansi that may perhaps be interpreted as a horn boss. Ringström also states in his diagnosis of *Chilotherium* that the frontal region is depressed, but this is not a constant character among the *Chilotherium* species. Among the Chinese Pontian *Chilotherium* species there is one, *Chilotherium planifrons* Ringström (1924: 47), in which the frontal region is flat, not depressed. The parietal crests are farther apart in the Chinese chilotheres than in the Loperot form, and the occiput is wider above (see Table 1). The premaxillaries of the Loperot rhinoceros are rather weak, and there are no remains of upper tusks in the collection, so that they were apparently edentulous, as is also the case in *Chilotherium*.

The Loperot skulls agree with those of the Chinese *Chilotherium* in the small distance between, and the position relative to the molars of, the orbit and nasomaxillary notch. Further they agree with *Chilotherium* in their separation of the inferior squamosal processes, and, above all, in the details of their dental structure, such as the hypsodonty combined with flattening of the ectolophs, the marked constriction

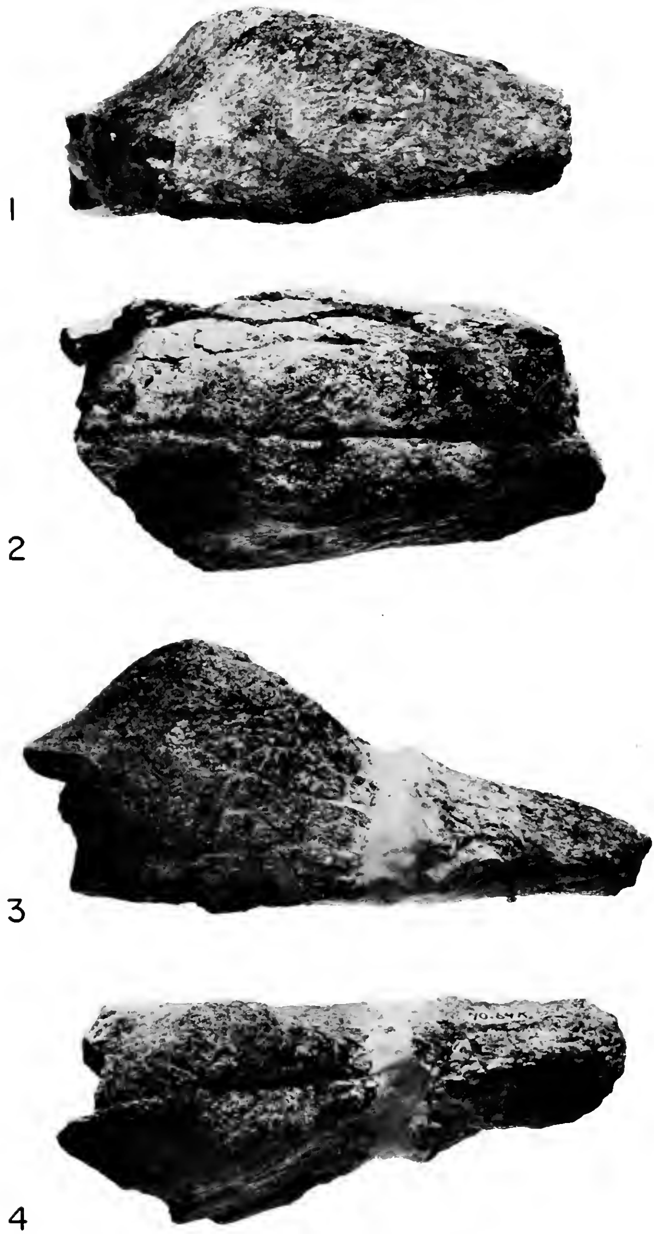

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Plate 5. *Chilatheridium pattersoni.* Figs. 1–2, nasals of skull No. 1 (70–64K, C9–10); figs. 3–4, isolated nasals (70–64K). Right and top views. × 0.70.

TABLE 2. Measurements of the upper dentitions from Loperot (in mm)

	Skull No. 1	Skull No. 2	
P^2, a. -p.	31	—	
tr., ant.	31	*ca.* 35	
tr., post.	35	*ca.* 40	
P^3, a. -p.	33	—	
tr., ant.	45	*ca.* 45	
tr., post.	48	—	
P^4, a. -p.	42	—	
tr., ant.	58	—	
tr., post.	56	—	
M^1, a. -p.	—	—	
tr., ant.	64	*ca.* 60	
tr., post.	—	—	
M^2, a. -p.	57	*ca.* 55	
tr., ant.	—	*ca.* 70	
tr., post.	—	*ca.* 65	Loperot 1948
M^3, a. -p. (internally)	*ca.* 57	*ca.* 55	56
tr., ant.	—	*ca.* 60	60
length outer surface	62	—	61

of the protocone, the antecrochet development, the weakness of the crista, if any, and the metacone bulge in M^3.

The great length from occipital crest to front of orbit, as seen in Table 1, would seem to differentiate the Loperot skull from those recorded by Ringström. However, the relative length in the Loperot form is not greater than that in all of the Chinese species. It is true that in two skulls of *Chilotherium anderssoni* Ringström fully as long as the Loperot skull (*ca.* 510–*ca.* 520 mm in occipitonasal length), the distance from occipital crest to front of orbit is only 310–322 mm, as opposed to 360 mm in Loperot skull No. 2. However, in the skull of *Chilotherium planifrons* the occipitonasal length is *ca.* 445 mm, and the length from occipital crest to front of orbit is 300 mm (Ringström, 1924: 54), that is, two-thirds the occipitonasal length (*ca.* 0.67), equal to that in the Loperot skull (*ca.* 0.69).

There remain, therefore, several important cranial differences between the Loperot rhinoceros and the Chinese species of *Chilotherium*. In the Loperot form a weak median nasal horn is present in three out of three specimens, whereas in the chilotheres, nasal horns, if any at all, are the exception rather than the rule. The unpneumatized frontals and parietals, and the wider occiput and greater distance between the parietal crests set *Chilotherium* off from the Loperot form.

It is of interest to observe that the Loperot rhinoceros, with respect to the narrowness of the skull, rather resembles the Chinese forms referred to the genus *Diceratherium* (*palaeosinense* Ringström, 1924, and *tsaidamense* Bohlin, 1937). The width of the upper portion of the occiput is 98–129 mm in *Diceratherium*, and the least width between the parietal crests 10–31 mm (Bohlin, 1937: 64–65), both ranges that include the observations on the Loperot form (cf. Table 1). However, the Loperot rhinoceros cannot be referred to *Diceratherium* because it is not hornless (? female), nor does it have a transverse pair of horns on its nasals (? male). The dentition of the Loperot form is fully as hypsodont as in *Chilotherium*, and not subhypsodont as in *Diceratherium*. In the latter genus, moreover, the inferior squamosal processes enclose the subaural chan-

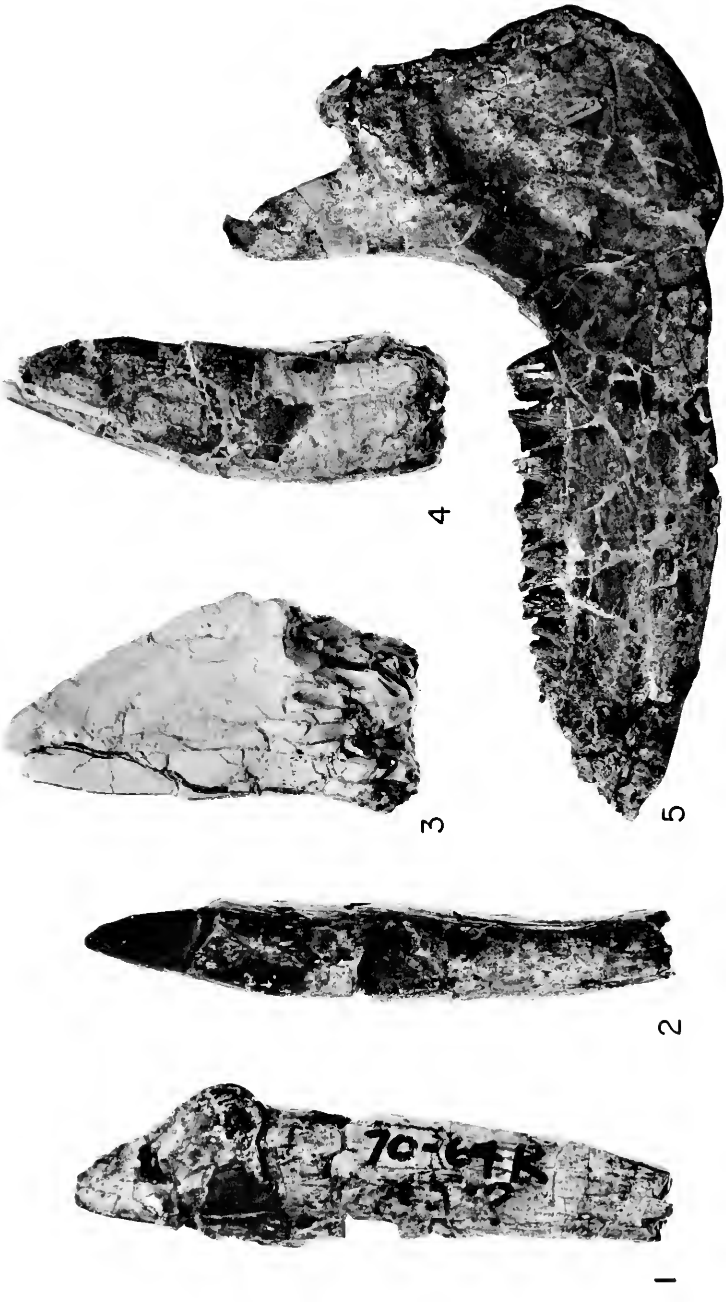


Plate 6. *Chilotheridium pattersoni.* Figs. 1–2, left lower canine (70–64K, 65), top and outer views, × 0.73. Fig. 5, right half of mandible No. 3 (70–64K, B11), inner view, × 0.22. *Chilotheridium* sp. cf. *C. pattersoni*, Kirimun, Kenya. Figs. 3–4, left lower canine (N.M.K. no. 33, 1949), top and outer views, × 0.69.

nel. This all apart from the fact that the reference of the Chinese forms to *Dicera-therium* is provisional and subject to revision (Ringström, 1924: 120; Bohlin, 1937: 98).

There are no mandibles in the Loperot collection associated with the crania described, but there are three isolated ones, all broken in the symphysial region, as well as two halves and two isolated lower canines. The mandibles, like the skulls, are extremely fragmented and distorted; plaster and plastic have been used to hold the specimens together in one piece. Some of the specimens of the lower jaw have been crushed sideways, and the symphysis is so deformed that width measurements cannot be given. Only in two specimens is enough of the symphysis preserved to permit measurements to be taken.

Mandible No. 1, labelled 70–64K, has been crushed from above downward; the ascending rami lack the coronoid process, and the condyle has been pressed down into the fragmented ramus so that its height above the lower border of the angle of the mandible is only some 185 mm, or roughly two-thirds that in the other mandibles, in which the height has not been so visibly reduced. The right canine of the mandible is lost, but its alveolus remains, while the left is broken off just inside its alveolar border. The cross section seen is a transverse oval, approximately 22 by 17 mm in diameter. The two canines are placed quite laterally in the symphysis, and there are no incisors or traces of alveoli between them. The symphysis widens to the front, but exact measurements cannot be given. The premolars and molars are all broken. An inner view of the left ramus with the distorted symphysis is given in Plate 7, figure 2.

Mandible No. 2 (70–64K, 65) has the symphysis laterally compressed, and shows parts of the two canine alveoli, although it is impossible to measure them. The space between the two rami is only a centimeter or two, and the ascending portions, restored from fragments, are very unequal: the right is a full 7 cm higher (from condyle to angle) than the left. The cheek teeth are characterized by the smallness of P_2, the external groove between the lophids of P_3–M_3 being well defined, and the absence of an external cingulum.

Mandible No. 3 (70–64K, B11) lacks the ascending ramus on the left side. The symphysial region is deformed, but a few measurements can be given. The symphysis widens slightly to the front, as it does in mandible No. 1 as well. The left ramus with the symphysis is presented in Plate 7, figure 1; the anterior two premolars from the right side are attached to this portion. An inner view of the right half of this mandible is given in Plate 6, figure 5.

Mandible No. 4 (70–64K, 65C) is quite complete on the right side, but it lacks the condyle. Of the left half of the same specimen only the portion bearing P_3 and P_4 is preserved. The forwardly expanding symphysis is incomplete in front, but the least width, at P_2, can be given.

Mandible No. 5 (70–64K, A18) consists of part of the left ramus, with P_2 and two complete molars.

The lower canine marked 70–64K, 65–? is well preserved (Pl. 6, figs. 1–2). It is of the left side, and the crown, worn to a height of 44 mm, is subtriangular in section. The internal edge is very sharp because of wear, the outer lower edge is rounded, and the upper outer edge marked by a longitudinal ridge. The base of the crown is slightly swollen lateroventrally. The dimensions at the crown base are 30 mm horizontally and 18 mm vertically. The enamel is very thin, especially on its upper surface. The root, a transverse oval 25 by 18 mm in cross section below the crown, becomes nearly round in section at the (broken) apex (15 by 14 mm); its length as preserved is 70 mm. This is just about the size of the smallest three lower canines of *Chilotherium anderssoni* as recorded by Ringström (1924: 37: 28–30 by 18–19 mm).

The other isolated lower canine (70–64K,

Plate 7. *Chilatheridium pattersoni.* Fig. 1, left half of mandible No. 3 (70–64K, B11), outer view, × 0.31. Fig. 2, left half of mandible No. 1 (70–64K), inner view, × 0.19. Fig. 3, right maxillary with dm^1, P^{2-3}, dm^4, M^1, crown view, × 0.38.

TABLE 3. Measurements of the mandible from Loperot (in mm)

	No. of specimen 1	2	3	4	*Chilotherium* China (Ringström, 1924)
Height from condyle to lower border of angle	—	*ca.* 265	*ca.* 250	—	215–231
Length from posterior border of C to that of angle	*ca.* 530	*ca.* 520	*ca.* 490	*ca.* 480	415–485
Height of ramus at M_3	—	*ca.* 90	*ca.* 95	*ca.* 100	76-*ca.* 90
Width of ramus at M_1	—	*ca.* 40	*ca.* 40	—	40–50
Median length of symphysis	*ca.* 150	—	*ca.* 130	—	104–137
Width of symphysis at P_2	—	—	—	*ca.* 80	98–128
Anterior width of symphysis	*ca.* 100	—	*ca.* 110	—	130–*ca.* 190
Distance between C at alveoli	*ca.* 45	—	*ca.* 60	—	75–93
Diastema C–P_2	—	—	*ca.* 50	—	55–96

A16) is not as well preserved. It is from the right side, measures 30 by 15 mm at the crown base, and is, therefore, more depressed from above downward than the left canine. The worn crown is 55 mm high, and there is a basal cingulum and a ridge along the dorsolateral edge. The inner edge of the crown is, again, sharp because of wear on the upper surface.

TABLE 4. Measurements of the lower dentitions from Loperot (in mm)

	No. of specimen 1	2	3	4	5
P_2, a. -p.	—	22	25	—	23
tr.	—	15	—	—	14
P_3, a. -p.	—	34	—	—	—
tr., ant.	—	20	—	18	—
tr., post.	—	21	—	21	—
P_4, a. -p.	—	38	—	—	—
tr., ant.	—	26	—	25	—
tr., post.	30	26	—	28	—
M_1, a. -p.	—	—	—	—	46
tr., ant.	—	*ca.* 26	—	28	—
tr., post.	—	—	—	29	26
M_2, a. -p.	—	58	57	53	—
tr., ant.	—	29	28	28	—
tr., post.	32	31	32	30	—
M_3, a. -p.	—	57	60	53	—
tr., ant.	—	29	30	27	—
tr., post.	29	28	28	27	—

It will be observed that, in keeping with its narrow cranium, the Loperot rhinoceros has a mandible that is narrower than that in the Chinese chilotheres. Further, although the height and the length of the jaw, as well as the symphysial length, may be greater in the Loperot form than in *Chilotherium* from China, there is no difference in proportions. The ratio of the height to the length of the mandible in Nos. 2 and 3 (the only ones in which both of these dimensions can be given approximately) is *ca.* 0.51; two mandibles of *Chilotherium anderssoni* give 0.48 (218:445) and 0.52 (231:443) respectively (Ringström, 1924: 54). The length of the symphysis in mandibles No. 1 and 3 is 0.27–0.28 (approximately) of the total length; in the Chinese chilotheres this ratio varies from 0.25 (in *Chilotherium habereri* var. *laticeps* 104:415) to 0.29 (in *Chilotherium anderssoni* 128:443) (Ringström, 1924: 54). In the narrow symphysis the Loperot rhinoceros approaches the Chinese *Diceratherium* (distance between C at alveoli 24–45 mm; width of symphysis 75–95 mm: Bohlin, 1937: 70), but in these Chinese forms the symphysis does not widen to the front, P_2 is relatively larger, and the coronoid process is stronger (cf. Ringström, 1924: 109–110; Bohlin, 1937: 71).

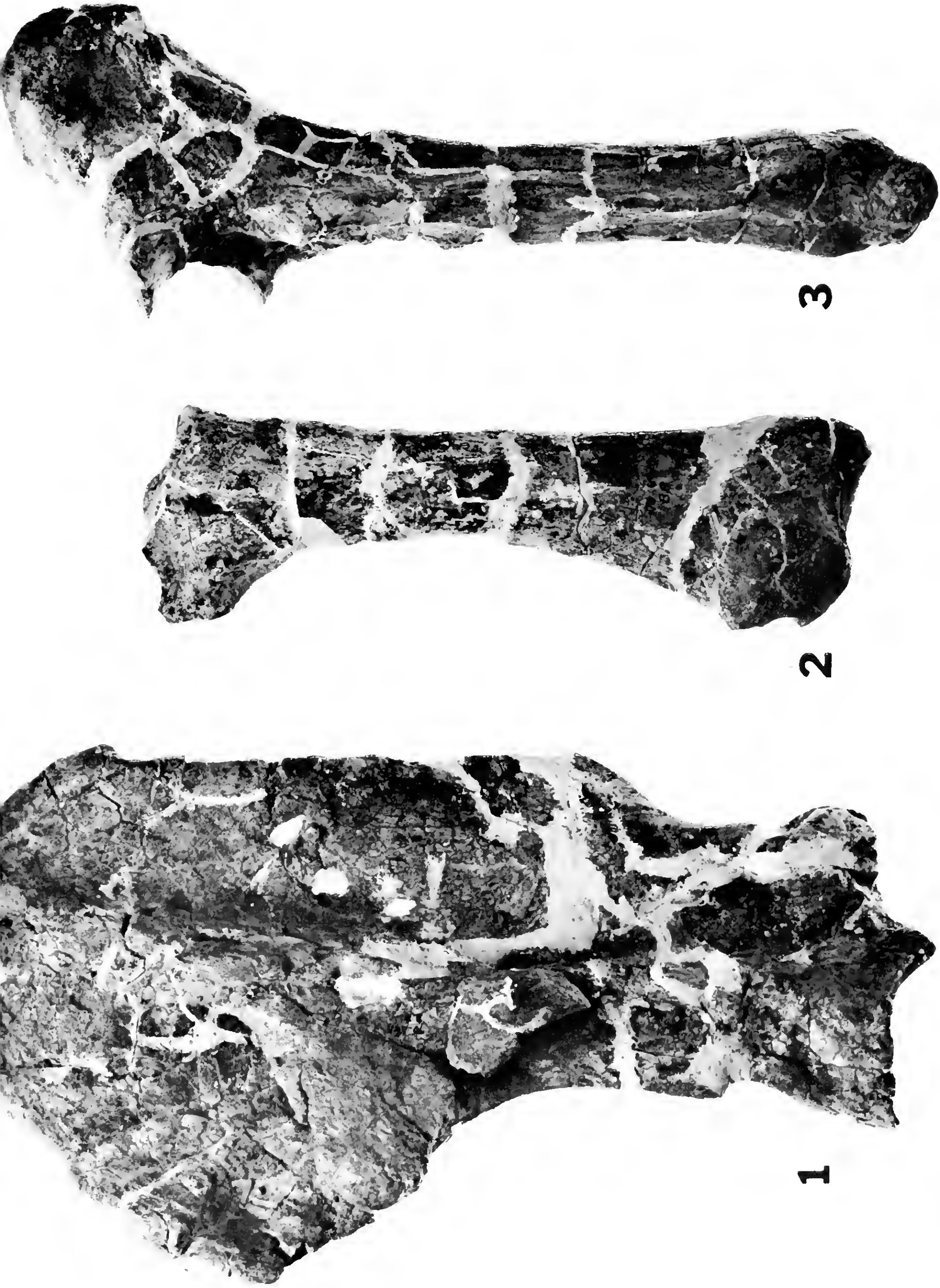


Plate 8. *Chilotheridium pattersoni.* Fig. 1, right scapula, No. 2 (70–64K, BB), lateral view. Fig. 2, right radius, No. 1 (70–64K, BB), lateral view. Fig. 3, right ulna, No. 1 (70–64K, A17), lateral view. × 0.33.

CHILOTHERIDIUM FROM EAST AFRICAN SITES OTHER THAN LOPEROT

Rusinga Island: Gumba and Wakondu

Two incomplete upper molars in the National Museum Centre for Prehistory and Palaeontology, Nairobi, originating from Gumba and Wakondu, respectively, have been described as *Chilotherium* sp. (Hooijer, 1966: 151, pl. 6, figs. 10 and 11), an identification that in the light of the Loperot discoveries may now be changed to *Chilotheridium* sp. Whether the Rusinga molars are specifically the same as those from Loperot must remain uncertain. While most of the vertebrate fossils from Rusinga come from strata about 18 m.y. old, age estimations of the formations on the Gumba Peninsula must be deferred until the completion of the study by Van Couvering and Miller (1969).

Kirimun, Kenya

The tip of a lower left canine from Kirimun in the collection at the National Museum Centre for Prehistory and Palaeontology, Nairobi (no. 33, 1949), is heavily worn and rather flattened horizontally (Pl. 6, figs 3–4). The vertical diameter at crown base is 25 mm, the horizontal diameter at least 40 mm. At the inner edge wear has produced a sharp angle. The enamel is thin but is present externally and ventrally. The tip is broken; the crown length as far as preserved is 60 mm. Very little more than the crown is preserved, but the root seems to assume a round cross section. The shape of the crown is as in *Chilotheridium* from Loperot, but the Kirimun specimen is larger; in size it is larger than all but one of the lower canines of *Chilotherium anderssoni* recorded by Ringström (1924: 37), which measures 47 by 26 mm.

Chilotheridium is not the only genus of rhinoceroses present at Kirimun. Among the bits of teeth from this site, collected during the Harvard Kenya Expedition of 1963 and sent to me for identification by Professor Bryan Patterson, there are part of an M_3 and part of a DM^3 or DM^4 referable to either *Aceratherium* or *Dicerorhinus*. The posterior half of an RM_3 (39–63K) from Kirimun, 27 mm wide, is worn to a height of 24 mm. Direct comparison with M_3 of *Aceratherium acutirostratum* (unworn height 30 mm) shows the same marked crownward taper of the sides of the postero-internal column and the same marked postero-external angle of the crown. In the Loperot M_3 the crown is higher (unworn height 50 mm), and, consequently, the crownward taper is less; the postero-external crown angle is less angular, too. The antero-external portion of a DM^3 or LDM^4 from Kirimun (25–63K), having thin enamel and showing the parastyle fold and paracone style, can be matched in the homologous teeth of *Dicerorhinus leakeyi* and *Aceratherium acutirostratum* from Rusinga described before (Hooijer, 1966: 134 and 142). Whether the second species of rhinocerotids from Kirimun represents *Aceratherium* or *Dicerorhinus* cannot be made out on the basis of this meagre material.

The Kirimun locality, at latitude 00° 43′N, and longitude 36° 54′E, is considered either late Miocene or early Pliocene by Leakey (*in* Bishop, 1967: 47).

Bukwa II, Uganda

Early in 1969 Dr. Alan Walker sent me casts of a number of teeth in the Uganda Museum, Kampala, excellently prepared by him and identified as *Chilotherium* sp. nov. (Walker, 1968, 1969). The specimens originate from the site Bukwa II on the northeast slopes of Mt. Elgon (Masaba), at latitude 01° 17′N, longitude 34° 47′E, and the capping lava has been dated at 22 m.y. The teeth, illustrated in Walker (1968), do agree with their homologues in the Loperot collection in all their diagnostic characters. There are teeth evidently of a single individual: a RP^2 incomplete internally and a LP^2 lacking the posterior outer corner and an inner portion of the protoloph; a RP^4 with an external height of 25

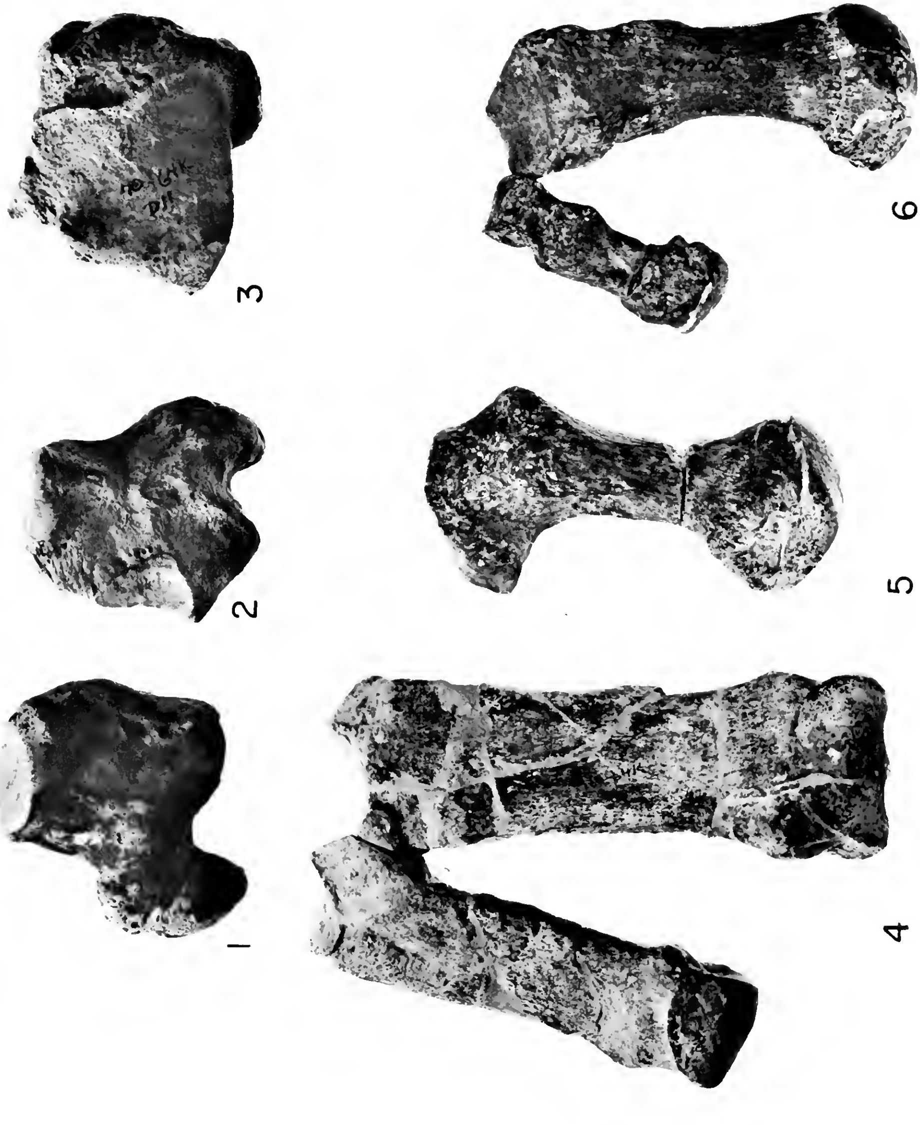


Plate 9. *Chilatheridium pattersoni.* Figs. 1–2, right entocuneiform, No. 1 (70–64K), and left entocuneiform, No. 2 (70–64K, D11), lateral views, × 0.70. Fig. 3, left metatarsal IV, No. 3 (70–64K), proximal view, × 0.90. Fig. 4, left metacarpal II, No. 2 (70–64K, A17), and left metacarpal III, No. 4 (70–64K, A17), articulated; front view, × 0.50. Fig. 5, right metacarpal V, No. 1 (70–64K, B14), lateral view, × 0.73. Fig. 6, the same articulated with right metacarpal IV, No. 1 (70–64K, B14), front view, × 0.50.

TABLE 5. Measurements of teeth of *Chilotheridium* from Bukwa II (in mm)

P^2, a.-p.	29	M^1, a.-p.	52	P_3, a.-p.	34
tr., ant.	34	tr., ant.	67	tr., ant.	20
tr., post.	*ca.* 39	tr., post.	64	tr., post.	23
P^4, a.-p.	40	M^2, a.-p.	61	P_4, a.-p.	37
tr., ant.	58	tr., ant.	74	tr., ant.	25
tr., post.	56	tr., post.	63	tr., post.	28

mm as worn, with the medisinus just closed off internally, very marked protocone folds as well as an anterior fold in the metaloph, an inner cingulum just a little less developed than that in P^4 of Loperot skull No. 2; an RM^1 worn down to 20 mm from the base externally, and an RM^2 nearly 30 mm high at the ectoloph, both showing an internally flattened, constricted protocone and an anterior metaloph fold, the powerful antecrochet, and the flattened ectoloph behind the (only) style, the paracone style, very weak so near the base, and the internal cingulum barely indicated at protoloph and metaloph but present at the medisinus entrance as a cusp. The P^2, as observed by Walker (1968: 155), has an anterior contact facet indicating the presence of a tooth, which must have been DM^1 also demonstrable in Loperot skull No. 1. Both P^4s (illustrated in the position of P^3 in Walker, 1968, plate) and the M^1 show what appears to be a very weak external cingulum, almost invisible on the casts. Of the mandible there are RP_{3-4} and the posterior portion of LM_3. Measurements of the Bukwa II teeth (Table 5) are very close indeed to those of the Loperot teeth (cf. Tables 2 and 4). The M_3 fragment has a posterior width of 31 mm, slightly greater than that in Loperot specimens (27–29 mm). The Bukwa site may be taken as early Miocene, even very early at that (Walker, 1968: 155).

The Bukwa II material described above is indistinguishable from that of Loperot, but although the generic position is certain (*Chilotheridium*) the specific identity of the two forms is a matter of conjecture. There is a second genus of rhinoceros at Bukwa II, identified by Walker (1968, 1969) as *Dicerorhinus* sp. (I have not seen this material). An incomplete right astragalus is all we have of postcranial material of rhinocerotids at Bukwa II, and a cast of it has been kindly sent to me by Dr. Walker. It lacks the medial ridge of the trochlea as well as the medial portion of the facet for the navicular, so that the medial height, the total width, and the widths of the trochlea and of the distal facets cannot be taken. The lateral height of the Bukwa II astragalus is 63 mm. It is impossible, even by direct comparison with the astragali of *Chilotheridium* of Loperot (this paper, p. 377) and with those of *Dicerorhinus* and *Aceratherium* (Hooijer, 1966: 173), to determine to which of these genera the Bukwa II bone should be referred. So, pending the discovery of postcranial material at Bukwa II that will prove to be identical with that of Loperot, the specific identity of the Bukwa II *Chilotheridium* with that of Loperot must remain uncertain.

Ngorora, Kenya

Late in 1968 Dr. W. W. Bishop entrusted to me the rhinoceros remains collected by him that year in the Ngorora Formation, Kenya, at latitude 00° 53′N, longitude 35° 51′E, approximately 10 m.y. old, i.e., early Pliocene. The rhinoceros remains were all picked up from the surface and are rather fragmentary. However, there is material of *Chilotheridium* again in this lot, dental as well as postcranial, which justifies the inclusion of the Ngorora material in the present paper.

To begin with, there is a right maxilla with DM^1, P^{2-4} and M^1, marked in the field 2/13.S. The tooth crowns are much worn and damaged internally as well as externally. No measurements can be given of either DM^1 or P^2. P^3 is *ca.* 45 mm anterotransversely, and P^4 is *ca.* 55 mm wide anteriorly, and *ca.* 52 mm wide behind, close to the Loperot teeth (Table 2). In

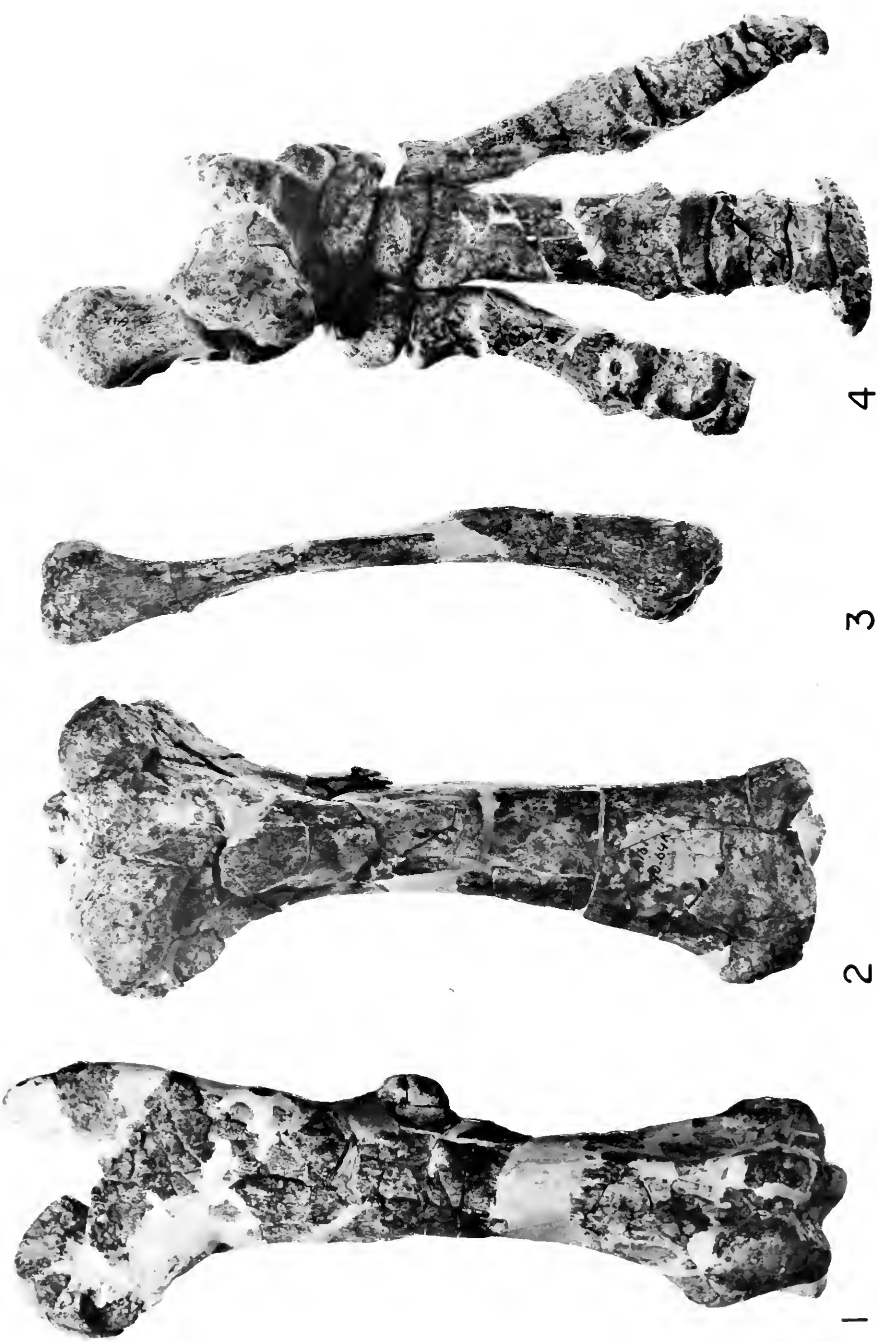


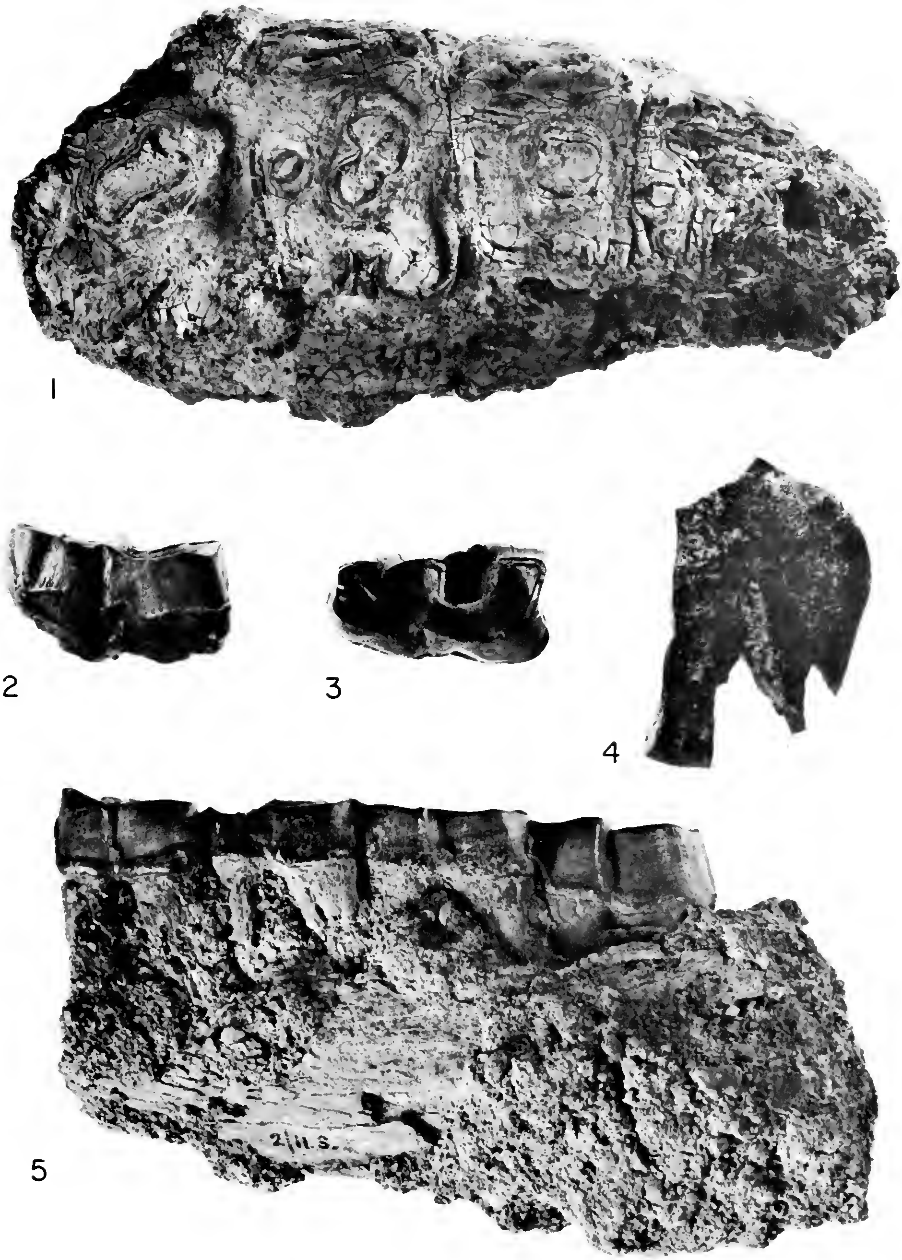
Plate 10. *Chilotheridium pattersoni.* Fig. 1, left femur, No. 1 (70–64K), front view, × 0.24. Fig. 2, right tibia, No. 1 (70–64K, A16), front view, × 0.32. Fig. 3, right fibula, No. 1 (70–64K, 65C), lateral view, × 0.32. Fig. 4, right pes, No. 1 (70–64K, B15–16), front view, × 0.32.

P^3 the medisinus remains only as an enamel island, the postsinus having been worn off completely. In P^4 both the medisinus, showing a weak crochet, and the postsinus remain as enamel islands. The posterior portion of the ectoloph is preserved in P^4, and it shows the flatness characteristic of *Chilotheridium* molars, there being no metacone style. The entrance to the medisinus has a cingular cusp slightly less developed than that in Loperot skull No. 1; the internal cingulum is weakly developed along the protoloph, too. The posterior protocone fold as well as the anterior metaloph fold can be seen distinctly; the antecrochet extends all across the medisinus. The M^1 is so much worn down and incomplete externally and internally that no measurements can be given; it shows, however, the anterior protocone fold (Pl. 11, fig. 1).

In the lot labelled 2/13.S there are further a number of fragments of an upper dentition, some of which are more characteristic than others. The RP^4 is the most complete specimen; it comprises most of the ectoloph and the external portion of the protoloph, and further, the inner portion of the metaloph not fitting on to the remainder of the crown. The ectoloph of P^4 is worn to a height of 49 mm and measures 42 mm anteroposteriorly. The paracone style is there, but effaced near the crown base, and there is no metacone style, the posterior half of the outer surface being flat, just as in the P^4 of Loperot skull No. 1 that is slightly more worn down. The portion of the protoloph preserved bears a well-developed cingulum. The anterior metaloph or hypocone fold is seen in the detached fragment; the protocone is not preserved in this specimen.

To the same individual appear to belong the posterior portions of the ectolophs or RM^1 and RM^2, both showing the absence of the metacone style. This makes the posterior portion of the ectoloph flat or even concave apically. The antero-external portion of an unworn LM^3 fortunately is present in the collection as well. The Ngorora cheek teeth show the hypsodonty by which *Chilotheridium* is characterized, notably the M^2 (Pl. 11, fig. 4). This dentition as a whole is a little less worn down than that of Loperot skull No. 1, the (worn) heights of P^4, M^1 and M^2 (49, 43, and 68 mm, respectively) being somewhat greater than those in Loperot skull No. 1 (45, 40, and 60 mm, respectively). The portion of LM^3 lacks the base, so that the full height cannot be determined; it is broken off anteriorly along the cingulum, which is highest in the depression into which fits the metastyle of M^2, 20 mm below (rootward of) the unworn edge. In the slightly worn M^3 of Loperot skull No. 1 the anterior cingulum is about 15 mm below the worn edge so that some 5 mm may be added to get the full crown height, which may be, then, 75 mm. Among the smaller fragments in lot 2/13.S there is one showing the posterior protocone fold being curved inward toward the base, as is characteristic of *Chilotheridium* molars. The other bits preserved are not characteristic one way or the other. In the lot 2/11.S there is an internal fragment of LM^3, rather worn, with the characteristic antecrochet, limited by the posterior protocone fold curving inward basally. In lot 2/11A.S there is a protoloph portion of a left upper molar with the strong anterior cingulum as well as the anterior protocone fold, and the inner surface of the protocone shows the characteristic flattening.

Although at the moment of writing we do not have any better preserved upper molars from Ngorora, the marked hypsodonty as seen in M^2, the flattened posterior ectoloph portions, the strong anterior cingulum, the inwardly curving posterior protocone folds, and the internal flattening of the protocone are absolutely diagnostic of *Chilotheridium*. In *Aceratherium* we find constricted protocones, too, but these are not flattened internally, and the molars are low crowned, the height of the outer surface of M^3 (unworn) in *Aceratherium*



late 11. *Chilotheridium pattersoni*. Fig. 1, right maxillary with dm^1, P^2–M^1 (2 13.S), crown view, × 0.75. Fig. 4, RM^2, osterior portion of ectoloph (2/13.S), outer view, × 0.60. *Brachypatherium* sp. Figs. 2–3, L dm_3 (2 2.S), outer and crown iews, × 0.67. *Aceratherium* c. q. *Dicerorhinus* sp. Fig. 5, left ramus with P_1–M_3 (2 11.S), outer view, × 0.55. All from Igorora, Kenya.

TABLE 6. Measurements of lower teeth of *Acerатherium* and *Dicerorhinus* (in mm)

	Ngorora 2/11.S	Ngorora 2/14.S	Ngorora 2/1.SL	Rusinga, Karungu, and Moruorot
P_2, a. -p.	—	25	26	26–28
tr.	—	18	18	17–22
P_3, tr., post.	—	25	—	22–24
P_4, a. -p.	38	37	—	35–39
tr., ant.	26	25	24	24–26
tr., post.	29	28	27	25–30
M_1, a. -p.	—	—	—	41–44
tr., ant.	28	—	—	26–29
tr., post.	30	30	—	28–31
M_2, a. -p.	45	49	—	41–50
tr., ant.	29	29	—	26–32
tr., post.	30	31	—	27–31
M_3, a. -p.	47	—	—	44–53
tr., ant.	28	—	—	27–31
tr., post.	28	28	—	26–29

acutirostratum being only 49 mm by a length of 65 mm (Hooijer, 1963: 43).

Lower teeth in the Ngorora collection at present available do not show the hypsodonty by which *Chilotheridium* is characterized: in the lot 2/14.S an unworn posterior lophid of RM_3 is only 30 mm high, against 50 mm in mandible No. 3 from Loperot. In lot 2/11.S there are a left ramus of the mandible with P_4–M_3 and a right ramus with $M_{2\text{-}3}$ of the same individual (Pl. 11, fig. 5). All the teeth are worn, and there are external cingula in the groove between the lophids of P_4, M_1 and M_2, which are short ridges placed 7–8 mm above the crown bases. The external grooves are well marked as in *Aceratherium* or *Dicerorhinus*, unlike what we find in advanced brachypotheres, where the external grooves are flattened out. In lot 2/14.S there are, all isolated but evidently belonging to one individual, P_2 from both sides, RP_3 incomplete in front, RP_4, the posterior part of RM_1, RM_2, and the posterior portion of RM_3. In this lot there are no external cingula except in M_2, a few cusplets down near the base of the external groove. There are further a RP_2 and a LP_4 in lot 2/1.SL, the external part of a lower P in 2/1.SU, and the posterior portion of a left lower molar, either M_1 or M_2, in lot 2/11.A.S., the latter unworn and with a full height of 40 mm. In Loperot mandible No. 3 a worn M_2 has just this height, and therefore was higher when unworn. Measurements (Table 6) show the Ngorora lower teeth to be similar to those of Loperot (Table 4) in size, except for the lengths of M_2 and M_3, which are greater in the Loperot mandibles. The Ngorora teeth, of course, are also less high crowned than those of Loperot, as stated above. As shown in Table 6 the Ngorora teeth are well within the variation limits of the mandibular teeth of *Aceratherium* and *Dicerorhinus* previously recorded from Rusinga, Karungu, and Moruorot (after Hooijer, 1966: 131, 133 and 141; 1968a: 234).

The lower teeth of *Dicerorhinus leakeyi* and *Aceratherium acutirostratum* are indistinguishable, and there are no differences between these and the Ngorora lowers. The lower teeth from Loperot are more hypsodont, as we have seen, and M_2 and M_3 are somewhat longer than those from Ngorora.

There is a lower milk molar in the Ngorora collection, a left DM_3 marked 2/2.S (Pl. 11, figs. 2–3) characterized by its thin enamel and the presence of a weak but continuous cingulum externally. External cingula may develop in *Brachypotherium* lower molars (see Roman and Viret, 1934: pl. X). Our *Brachypotherium heinzelini* from Congo, Kenya, and Uganda does not show a cingulum on its lower molars so far as known, and lower milk molars of this species have not yet been found. In size the Ngorora DM_3 exceeds that of *Brachypotherium brachypus* (Lartet) from La Grive-Saint-Alban; dentally there is no great difference between this species and *B. heinzelini* (Hooijer, 1966: 144), and therefore the Ngorora milk molar would seem to be too large to be referred to the latter species. In a collection from Lothagam Hill, Kenya, shortly

TABLE 7. Measurements of DM_3 of *Brachypotherium* sp. (in mm)

	Ngorora	Lothagam Hill
DM_3, a. -p.	46	43
tr., ant.	21	21
tr., post.	24	23

to be published upon by Professor Patterson and myself, and dating back approximately 5 million years, there is a large species of *Brachypotherium,* and its DM_3 is rather similar in dimensions and has a weak external cingulum as well. Measurements are given in Table 7.

The postcranial material from Ngorora, scanty as it is, belongs to *Chilotheridium* only. There are the proximal and distal parts of a right radius and a phalanx, both labelled 2/11.S. The radius is *ca.* 90 mm wide proximally by a shaft width of *ca.* 46 mm, and a width of the distal facets of 80 mm. These dimensions are as in *Chilotheridium* from Loperot (Table 8), and the presence of a small, lateral facet for the cuneiform unequivocally shows the Ngorora radius to belong to this genus. The phalanx is the first of a median digit, with a length of 33 mm and a proximal width of 46 mm, of the same size and proportions as in the Loperot *Chilotheridium* (p. 385).

Since we have both dental and postcranial material from Ngorora that is indistinguishable from that of Loperot, it would seem justified to accept not only generic but also specific identity of the rhinoceros from the two localities.

POSTCRANIAL SKELETON OF *CHILOTHERIDIUM PATTERSONI* GEN. ET SP. NOV.

There are two specimens of the atlas in the Loperot collection, one (70–64K, 65B) nearly complete, the other (70–64K, C1) lacking the dorsal arch and much distorted. The greatest width of the first specimen is 285 mm, the width across the occipital articular facets 130 mm, the distance between the intervertebral foramina in the dorsal arch 93 mm, and the mid-ventral length (including the median posterior tubercle *ca.* 20 mm long and wide) *ca.* 65 mm. These data do not differ much from those of the atlas of *Chilotherium anderssoni* (Ringström, 1924: 55; Bohlin, 1937: 72), but the atlas of *Aceratherium acutirostratum* (Hooijer, 1966: 158) is not so very different either.

Of the scapula we have a series of five specimens, two of which are rather complete although they are fragmented (70–64K, A18, and 70–64K, BB, from the left and from the right side, respectively), and three specimens all from the right side (70–64K, BL, 70–64K, 65B, and 70–64K, BB) lacking most of the borders and of the spine; the last specimen is a proximal portion only.

The thickened vertebral or upper border is best preserved in scapula No. 2; it is highest at the point where the spina scapulae ends and is regularly convex. It forms an angle behind, at two-thirds of the height from the anterior border of the glenoid cavity, where it passes into the thin posterior border, which is concave throughout. The anterior border of the scapula is likewise thin. It is straight for the most part in the reconstructed specimen No. 2 but was probably weakly convex in its upper three-fourths, the basal part being concave, forming the "neck," and becoming very thick where it ends in the massive tuber scapulae. The spina scapulae, running from the neck to the upper border, gives off a large, triangular, posteriorly directed tuber spinae, which extends just beyond the posterior border with its thick, rough extremity a little distance above the middle of the height of the bone. It is broken into fragments that are held together with plastic and plaster and is pressed against the infraspinous fossa, but it originally extended outward as well as backward. Its anteroposterior extent is 130–140 mm (the upper portion of the

TABLE 8. Measurements of radius from Loperot (in mm)

	No. of specimen									
	1	2	3	4	7	8	9	10	11	14
Median length	315	310	280	290	—	—	—	—	—	—
Proximal width	94	96	90	90	—	92	86	—	—	—
Middle width	*ca.* 50	*ca.* 45	*ca.* 45	*ca.* 45	—	—	—	—	—	—
Greatest distal width	95	95	—	*ca.* 100	—	—	—	—	—	—
Width distal facets	87	86	88	*ca.* 90	82	—	—	85	80	80

tuber spinae, preserved in scapula No. 1, is slightly longer than that in specimen No. 2). The total height, from the anterior border of the glenoid cavity to the end of the spine at the upper border, is 440 mm in No. 2; in No. 1 it is *ca.* 470 mm, but this measurement is too great because of the spaces between the fragments, filled with plaster. Likewise, the anteroposterior diameter of the neck, over 120 mm in No. 2, is too large; in No. 1 this diameter is 100 mm, which must be very nearly correct as there are no spaces between the bone fragments in this portion. The anteroposterior diameter over the glenoid cavity and tuber scapulae reads 120 mm in No. 1, and the anteroposterior and transverse diameters of the glenoid cavity are 80 mm and 70 mm in No. 2. The greatest anteroposterior diameter of the scapula is over 240 mm, as seen in No. 2. No more exact measurements can be given.

The scapula of *Chilotherium* from China, originally stated to be *ca.* 400 mm high and 93 mm wide at the neck (Ringström, 1924: 60 61), as a more complete specimen showed, is 478 mm high and 88 mm wide at the neck (Bohlin, 1937: 80). Our Loperot scapulae are less high, and wider at the neck (see above), while the tuber spinae is more developed than in *Chilotherium*, longer than the width of the neck. The scapula of *Dicerorhinus leakeyi* is likewise higher and slenderer than those of Loperot (Hooijer, 1966: 158), with a less developed tuber spinae, only 75 mm long and not extending to the posterior margin of the bone. A lateral view of Loperot scapula No. 2 is given in Plate 8, figure 1. The proportions of the Loperot scapula are very similar to those in the slightly smaller *Diceratherium* from China, of which the greatest height is 404 mm, the neck width 77–? 85 mm, and the greatest anteroposterior diameter 200–204 mm (Bohlin, 1937: 80 and fig. 120).

Humeri in the Loperot collection are very poorly preserved. There are three bones from the right side: 70–64K, A18, 70–64K, BB, and 70–64K. In No. 1 both ends are preserved, but no exact measurements can be given because of the crushing of the specimen. Number 2 lacks the proximal end, and in No. 3 the distal end is shattered. There is, in addition, No. 4, the distal trochlea of a right humerus, 70–64K.

The humerus of the Chinese *Chilotherium* (Ringström, 1924: 55 and 61) is shorter than that in fossil *Dicerorhinus* (Hooijer, 1966: 160), but less broad as well except in the greatest width at the distal end, which is proportionally greater in *Chilotherium* than in *Dicerorhinus*. It is unfortunate that the Loperot bones cannot be exactly measured; the length from caput to medial condyle in No. 1 would have been about 340 mm, like that in *Chilotherium* (345–353 mm), but the greatest distal width would not have exceeded 130 mm, which is less than that in the *Chilotherium* humeri (150 mm) but proportionally as great as that in *D. orientalis* and *D. primaevus* with a length of 370–400 mm and a greatest distal width of 160–167 mm.

TABLE 9. Measurements of ulna from Loperot (in mm)

	No. of specimen				
	1	2	3	5	9
Greatest length	420	*ca.* 400	*ca.* 390	—	—
Length from proc. anconaeus ("beak")	355	*ca.* 350	—	—	—
Length of olecranon from "beak"	145	*ca.* 125	*ca.* 125	135	—
Width at semilunar notch	90	80	—	*ca.* 80	—
Greatest distal diameter	62	60	66	—	60

The width of the distal trochlea is 90 mm in Loperot humerus No. 4, not greater than that in *Chilotherium.*

The following specimens of the radius are in the Loperot collection: 1) right radius, 70–64K, BB; 2) left radius, 70–64K, A16; 3) and 4) right and left radius, 70–64K, C14; 5) right radius without distal end, 70–64K, BB; 6) left radius without distal end, 70–64K, A17; 7) right radius in three parts, 70–64K, BB; 8) proximal portion of right radius, 70–64K; 9) proximal portion of left radius, 70–64K, E10; 10) distal portion of right radius, 70–64K; 11) distal portion of right radius, 70–64K, B16; 12) idem, 57–64K; 13) idem, 70–64K, C12; 14) distal portion of left radius, 70–64K, BB; and, 15) distal fragment of right radius comprising only part of the facet for the scaphoid, 70–64K. Measurements are given in Table 8.

These radii, especially Nos. 3 and 4, agree very well with those of *Chilotherium anderssoni*, *Diceratherium palaeosinense*, and *D. tsaidamense* in length and proximal and distal width (Ringström, 1924: 55 and 113; Bohlin, 1937: 82). The mid-shaft width is greater in *Chilotherium* (55–57 mm) than in *Diceratherium* (41–46 mm); in this respect the Loperot radii are nearer to *Diceratherium.* All the specimens in which the lateral portion of the distal end is well preserved show a very small facet for the cuneiform, set off at an obtuse angle from that for the lunar (Nos. 1–4, 7, 10–12, and 14). Such a facet, only 1 cm wide and 1½ to 2 cm anteroposteriorly, is found in *Chilotherium* as well as in the Chinese *Diceratherium* and in the American diceratheres (Ringström, 1924: 46 and 111; Bohlin, 1937: 82). It does not show in *Aceratherium* or *Dicerorhinus* (which have longer radii: Hooijer, 1966: 161), and not in the recent rhinoceroses either. Radius No. 1 is shown in Plate 8, figure 2.

The ulna is represented in the Loperot collection by the following specimens: 1) left ulna, 70–64K, A17; 2) right ulna broken at mid-shaft, 70–64K; 3) right ulna broken at mid-shaft, 70–64K, BB; 4) right ulna without distal end, 70–64K, BB?; 5) left ulna without distal end, 70–64K, C14; 6) left ulna, much broken, distal end missing, 70–64K, C14; 7) left ulna, olecranon and distal end missing, 70–64K, BB; 8) right ulna, olecranon and distal epiphyses missing, 70–64K, A17; 9) distal portion of right ulna, 70–64K, BB; 10) distal portion and part of shaft of right ulna, 57–64K; and, 11) distal portion of left ulna, 70–64K, BB. Few of these bones can be measured exactly.

Entire ulnae are not available either in the Chinese *Chilotherium* or in the Chinese *Diceratherium;* Ringström (1924: 55) gives the length of the ulna of *Chilotherium anderssoni* as 370–390 mm, with a least width of 33 mm. Our most complete specimen (No. 1) has a least width of *ca.* 45 mm; the specimen is figured in Plate 8, figure 3. It should be remarked that among the Loperot material there is no case of ankylosis of radius and ulna as we see in *Chilotherium* (Ringström, 1924: 56).

TABLE 10. Measurements of scaphoid from Loperot (in mm)

	No. of specimen					
	1	2	3	4	5	6
Posterior height	59	55	55	—	—	60
Anterior height	47	43	46	44	—	47
Proximal width	43	40	—	—	39	43
Distal width	52	43	—	—	—	52
Greatest distal diameter	71	*ca.* 67	—	—	—	70

Six specimens of the scaphoid[1] are in the Loperot collection, Nos. 1–5 are from the right side (marked consecutively 70–64K, A16; 70–64K; 70–64K, BB; 70–64K, D11; and 70–64K, BB), and No. 6 is from the left side (70–64K). Number 3 is incomplete laterally, No. 4 lacks the posterior half, and No. 5 is incomplete distally. Numbers 1 and 6 may well have belonged to one and the same individual. Measurements are in Table 10.

The Loperot scaphoids differ from those of *Aceratherium* and *Dicerorhinus* (Hooijer, 1966: 162) in that the distal outward projection, which bears on its distal surface the facet for the magnum, extends beyond the proximal radius facet, thus making the distal width greater than the proximal. This is most marked in Nos. 1 and 6, and less in No. 2. Further, the proximal projection behind the radius facet is much developed in Nos. 1 and 6, and not so in Nos. 2 and 3. In none of the specimens does the distal projection behind the trapezium facet extend downward beyond this facet, as it does in *Aceratherium* and *Dicerorhinus* to a certain extent. In all the fossil specimens the posterior height exceeds the anterior height (the latter measured over the convex anterior portion of the radius facet and the ridge between the facets for the trapezoid and the magnum), while these heights are nearly equal in *Dicerorhinus sumatrensis*. In this recent species the ratio of anterior height (55 mm) to greatest distal diameter (79 mm) is 70, which shows that the scaphoid is relatively higher than that in *Dicerorhinus ringstroemi* (see Hooijer, 1966: 162), in which this ratio is 66. In a specimen of *Diceratherium palaeosinense* this ratio is 62, and in a specimen of *Chilotherium* it is only 51 (Bohlin, 1946: 222). Our Loperot specimens give *ca.* 64–67 for this ratio, and therefore are not as low as the scaphoid in *Chilotherium* but appear to agree better with *Diceratherium* and *Dicerorhinus* in this respect.

The lunar is represented in the Loperot collection by four specimens, but none of these is entire, unfortunately. All lack the posterior downward projection. In No. 1, a right lunar (70–64K), there are at least the greater parts of the upper and lower lateral facets for the cuneiform, of the distal facet for the unciform, and of the medial facets for the scaphoid (anteriorly) and the magnum (posteriorly). The medial part of the proximal facet for the radius is broken off, and hence the proximal width cannot be given. Number 2, a right lunar (70–64K) is damaged anteriorly as well, but its proximal width can be given. Number 3, a right lunar (70–64K) consists merely of a lateral portion, and is injured posteriorly, lacking most of the radius facet. Number 4, a left lunar (70–64K), is nearly complete proximally but lacks the distal unciform facet. In all of these specimens there is no facet for the ulna, the proximal lateral facet for the ulna that we find in *Aceratherium* and *Dicerorhinus* (Hooijer, 1966: 162). As stated above, in these genera the radius does not show a distal lateral facet for the cuneiform, the ulna articulating (for a very

[1] In the nomenclature of the carpal bones British usage is adopted. The terms used are in the first column, below, and those used by Ringström (1924) and Bohlin (1937, 1946) appear in the second column.

scaphoid	Radiale
lunar	Intermedium
cuneiform	Ulnare
pisiform	Pisiforme
trapezium	Carpale I
trapezoid	Carpale II
magnum	Carpale III
unciform	Carpale IV & V

TABLE 11. Measurements of lunar from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Anterior height	38	*ca.* 35	30+	—
Proximal width	—	36	—	40

small part) with the lunar, cutting off the radius from contact with the cuneiform. The condition seen in the Loperot lunars is like that in *Chilotherium* and *Diceratherium* (Ringström, 1924: 56 and 111; Bohlin, 1937: 82).

Of the cuneiform we have twelve specimens in the Loperot collection; Nos. 1–7 are from the right side, and Nos. 8–12 from the left: 1) 57–64K; 2) 57–64K; 3) 70–64K, damaged proximally; 4) 68–64K, posterior half missing; 5) 68–64K, incomplete proximally and laterally; 6) 70–64K, incomplete distally; 7) 70–64K, A16, incomplete behind; 8) 68–64K; 9) 57–64K, incomplete behind; 10) 70–64K, BB; 11) 70–64K, incomplete behind; and, 12) 70–64K, incomplete in front and distally.

The cuneiform of *Chilotherium* as described by Bohlin (1946: 224) does not appear to have very distinctive characters: the depressions and swellings on the nonarticular surfaces vary individually, and so do the heights of the two facets for the lunar and the shape of the distal unciform facet. It is stated that the unciform facet is quadrangular rather than triangular because the anterolateral side of the bone is so strongly convex, but this varies individually, too: in No. 1 the facet is subtriangular, and in No. 2 it is rather quadrangular. In *Dicerorhinus* the cuneiform varies in these respects also.

Three proximal ends of pisiforms, marked 57–64K, 70–64K, and 70–64K, display the two small facets for the ulna and the cuneiform, set at right angles to each other, or slightly less than 90°. Bohlin (1946: 226) states that the angle between these two facets on the pisiform is distinctly obtuse in *Chilotherium*, whereas it is less than 90° in the American *Diceratherium*. Since the main part is missing in the Loperot pisiforms, the diameter over the two proximal facets may be given, which is 26 mm, 23 mm, and 24 mm in Nos. 1–3.

No trapezium has been recognized in the collection.

The trapezoid is represented in the Loperot collection by seven specimens, as follows: 1) right trapezoid, 70–64K, H11, incomplete posteriorly; 2) right trapezoid, posterior half only, 70–64K; 3) right trapezoid, 70–64K, damaged at both ends; 4) left trapezoid, 57–64K; 5) left trapezoid, 70–64K, A16; 6) left trapezoid, 57–64K; and, 7) left trapezoid, 70–64K, incomplete behind. Ringström (1924: 57) mentions the trapezoid of *Chilotherium* to be of the ordinary type; it is mentioned by Bohlin (1937: 82) to differ from that of the Chinese *Diceratherium* in the markedly oblique posterior surface. This *Chilotherium* feature does not show in the Loperot trapezoids. As seen in Table 13 the anterior width and height are nearly equal in Nos. 1 and 7, and very different in Nos. 4–6; the two trapezoids of *Diceratherium* (Bohlin, 1937: 84) vary in the same way. In *Chilotherium* (2 specimens:

TABLE 12. Measurements of cuneiform from Loperot (in mm)

	No. of specimen											
	1	2	3	4	5	6	7	8	9	10	11	12
Anterior height	45	42	—	47	—	—	43	45	42	43	42	—
Distal width	43	34	36	—	34	—	34	39	35	33	38	34
Proximal ant. post. diam.	33	31	—	—	29	32	—	34	—	30	—	—
Greatest horizontal diam.	51	44	49	—	47	—	—	48	—	46	—	—

TABLE 13. Measurements of trapezoid from Loperot (in mm)

	No. of specimen					
	1	2	4	5	6	7
Anterior height	*ca.* 26	—	30	29	30	26
Anterior width	28	—	24	22	25	25
Greatest ant. post. diam.	—	—	41	39	46	—
Posterior height	—	27	28	27	33	—
Posterior width	—	18	16	16	17	—

Bohlin, 1937: 84) anterior width and height of the trapezoid are nearly the same, and in one specimen the width exceeds the height, as in Loperot trapezoid No. 1.

In the earlier Miocene East African rhinoceros collection (Hooijer, 1966) the trapezoid was not represented; the trapezoid of *Dicerorhinus primaevus* Arambourg (1959: 67) has the same anterior height and anteroposterior diameter as Loperot No. 5, while the trapezoid of *Dicerorhinus sumatrensis* (same skeleton as that used in the 1966 paper) in anterior height and width (34 mm and 28 mm) as well as in posterior height and width (33 mm and 21 mm) exceeds all the fossil specimens, even though its anteroposterior diameter is only 38 mm.

The magnum is represented in the Loperot collection by no less than ten specimens, but none of these is entire. The posterior downward process is missing in all the specimens; it is separately preserved in Nos. 1 and 2 but cannot be fitted on to the remainder of the bone. The convex posterior facet for the lunar is broken off in all specimens except Nos. 1, 2 and 8, leaving just the front portion of the bone. In No. 10 this portion is incomplete laterally. Numbers 1–7 are from the right side, Nos. 8–10 from the left. They are marked as follows: 1) 70–64K, BB; 2) 70–64K, B14; 3) 70–64K; 4) 70–64K; 5) 57–64K; 6) 70–64K; 7) 70–64K; 8) 70–64K; 9) 68–64K; and, 10) 70–64K, H11. Measurements are given in Table 14.

The magnum of *Chilotherium* is described by Ringström (1924: 57) as large and wide with a small height; the magnum of *Diceratherium palaeosinense* is wider still (45 mm against 36–37 mm) by nearly the same height (23 mm against 20–22 mm), and that of *Diceratherium tsaidamense* is 36 mm wide and 26 mm high (Bohlin, 1937: 84). The ratio of height to width in the Loperot magnum series varies from 0.63 (in No. 1) to 0.75 (in No. 9); in *D. tsaidamense* and *D. palaeosinense* these ratios are 0.72, and 0.51, respectively, and in two *Chilotherium* specimens these values are 0.61 and 0.54. Thus, the *Chilotherium* magnum appears to be relatively wider than those from Loperot, and so is that of *Diceratherium palaeosinense*, while *D. tsaidamense* resembles the Loperot bones in relative height of the magnum. It is further worthy of note that two Rusinga magna (Hooijer, 1966: 164) are very close to that of *D. tsaidamense* in height (25–27 mm) and width (36–38 mm) but exceed it in greatest length (75–82 mm against only 67 mm).

Twelve specimens of the unciform are in the Loperot collection; all except No. 1 and No. 9 lack the posterior process. Numbers 2, 4 and 11 are incomplete laterally, and No. 8 is merely a mediodistal fragment. Numbers 1–8 are from the right side, and

TABLE 14. Measurements of magnum from Loperot (in mm)

	No. of specimen									
	1	2	3	4	5	6	7	8	9	10
Greatest anterior height	31	32	32	33	32	33	30	30	33	32
Greatest anterior width	49	44	48	47	47	45	44	44	44	—
Proximal ant. post. diam.	59	59	—	—	—	—	—	57	—	—

TABLE 15. Measurements of unciform from Loperot (in mm)

	No. of specimen										
	1	2	3	4	5	6	7	9	10	11	12
Greatest anterior height	47	45	38	43	43	42	42	42	45	43	39
Greatest width	57	—	47	—	47	47	51	46	51	—	54
Greatest ant. post. diameter	83	—	—	—	—	—	—	71	—	—	—

Nos. 9–12 from the left. Numbers 5 and 9 almost certainly belong to a single individual. The markings on the bones are as follows: 1) 70–64K, A17; 2) 57–64K; 3) 70–64K, J7; 4) 70–64K, A16, 17; 5) 70–64K; 6) 57–64K; 7) 57–64K; 8) 70–64K; 9) 70–64K, A16; 10) 70–64K, E11; 11) 70–64K; and, 12) 70–64K, D10.

The measurements in Table 15 indicate the variability in the Loperot series. In comparing these data with those of *Chilotherium* and *Dicerorhinus* as given by Bohlin (1946: 225), it should be remarked that the height anteriorly as given by this author and as shown in his illustrations is taken at right angles to the proximal facet for the lunar, which corresponds to what I use as greatest width. I take the greatest anterior height perpendicular to the straight portion of the distal surface articulating with metacarpal III and the medial portion of metacarpal IV, and from there to the top of the bone, which is the lateral end of the facet for the cuneiform. As can be seen from the front views of the bones in Bohlin (1946: 225, fig. 81), the greatest height is only *ca.* 35 mm in the largest of the two *Chilotherium* unciforms with a greatest width of 46 mm and a greatest anteroposterior diameter of 86 mm. The greatest height in an unciform of *Dicerorhinus ringstroemi* Arambourg (1959: 73; for *D. orientalis* Ringström, non Schlosser) from the Chinese Pontian is *ca.* 65 mm by a greatest width of 78 mm and a greatest anteroposterior diameter of 108 mm.

The ratio of anterior height to anterior width is *ca.* 0.76 in the *Chilotherium*, and *ca.* 0.83 in the *Dicerorhinus* specimen, a difference of no significance; in our Loperot series this height/width ratio varies from 0.72 in No. 12 to 0.92 in No. 5. The difference between *Chilotherium* and *Dicerorhinus* unciforms can be demonstrated in ratio of anterior width to greatest anteroposterior diameter; this was already shown by Bohlin (1946: 225, table). In *Chilotherium* (two specimens) the ratio is 0.53 and 0.57, whereas in *Dicerorhinus ringstroemi* this ratio is 0.71 and 0.72; in Recent *Dicerorhinus sumatrensis* (Hooijer, 1966: 164) the ratio is even 0.79. In their ratio of greatest width to greatest anteroposterior diameter the two entire Loperot unciforms are intermediate and even nearer to *Dicerorhinus* than to *Chilotherium*, the ratio being 0.65 in No. 9, and 0.69 in No. 1. It should finally be noted that the two Rusinga unciforms previously recorded (Hooijer, 1966: 164) are within the variation limits of the *Dicerorhinus* specimens, their ratios being 0.72 and 0.75.

In the Loperot collection there are a number of specimens of all four metacarpals, as follows:

Metacarpal II, 9 specimens: 1) right Mc. II, 70–64K, B13; 2) left Mc. II, 70–64K, A17; 3) right Mc. II, proximal portion, 70–64K, BB; 4) right Mc. II, proximal portion, incomplete laterally, 70–64K; 5) right Mc. II, proximal portion, incomplete behind, 70–64K; 6) right Mc. II, proximal portion, incomplete laterally, 57–64K; 7) left Mc. II, proximal portion, incomplete laterally, 70–64K; 8) left Mc. II, proximal portion, 70–64K, B14; and, 9) left Mc. II, proximal portion, 70–64K.

Metacarpal III, 5 specimens: 1) right Mc. III, 70–64K; 2) right Mc. III, proximal portion, incomplete behind, 57–64K; 3)

TABLE 16. Measurements of Metacarpals II–V from Loperot (in mm)

	No. of specimen				
Mc. II	1	2	3	7	8
Median length	123	123	—	—	—
Proximal width	41	42	43	43	47
Proximal ant. post. diameter	36	37	43	42	39
Middle width	33	*ca.* 33	36	—	—
Middle ant. post. diameter	17	15	18	18	—
Greatest distal width	43	37	—	—	—
Width of distal trochlea	37	32	—	—	—
Distal ant. post. diameter	37	37	—	—	—
Ratio middle width/length	0.27	*ca.* 0.27	—	—	—

	No. of specimen				
Mc. III	1	2	3	4	5
Median length	140	—	—	143	154
Proximal width	49	61	57	52	61
Proximal ant. post. diameter	38	—	—	40	44
Middle width	39	—	—	40	43
Middle ant. post. diameter	17	—	—	18	21
Greatest distal width	52	—	—	51	61
Width of distal trochlea	45	—	—	45	49
Distal ant. post. diameter	39	—	—	38	40
Ratio middle width/length	0.28	—	—	0.28	0.28

	No. of specimen				
Mc. IV	1	2	3	4	5
Median length	115	116	—	126	118
Proximal width	37	34	39	—	35
Proximal ant. post. diameter	44	41	43	—	42
Middle width	26	—	—	31	23
Middle ant. post. diameter	18	16	—	18	17
Greatest distal width	41	40	—	46	39
Width of distal trochlea	36	34	—	38	34
Distal ant. post. diameter	33	37	—	36	36
Ratio middle width/length	0.23	—	—	0.25	0.19

	No. of specimen				
Mc. V	1	2	3	4	5
Median length	71	71	70	82	—
Proximal width	18	20	17	22	18
Proximal ant. post. diameter	35	34	28	35	*ca.* 30
Middle width	17	18	15	19	—
Middle ant. post. diameter	12	13	12	15	—
Greatest distal width	28	28	26	32	29
Width of distal trochlea	25	25	21	31	24
Distal ant. post. diameter	25	24	23	25	23
Ratio middle width/length	0.24	0.25	0.21	0.23	—

right Mc. III, proximal portion, incomplete behind, 70–64K, B14; 4) right Mc. III, 70–64K, A17; and, 5) left Mc. III, 70–64K, A17.

Metacarpal IV, 5 specimens: 1) right Mc. IV, 70–64K, B14; 2) right Mc. IV, 70–64K, C14; 3) right Mc. IV, proximal portion, 57–64K; 4) left Mc. IV, damaged proximally, 70–64K, A17 (proximal half), and A16, 17 (distal half); and, 5) left Mc. IV, facet for Mc. V damaged, 70–64K, C14.

Metacarpal V, 5 specimens: 1) right Mc. V, 70–64K, B14; 2) left Mc. V, 70–64K, BB; 3) left Mc. V, 70–64K, C14; 4) left Mc. V, BB; and, 5) left Mc. V, portion at mid-shaft missing, 70–64K.

Of the Fort Ternan rhinoceros, *Paradiceros mukirii* (Hooijer, 1968b: 87), the only metacarpal available, Mc. III, is hardly distinguishable from its homologue in the Loperot *Chilotheridium pattersoni*, showing that metapodials alone are unreliable for specific (or generic) differentiation (see Hooijer, 1966: 153/54, and above, p. 340).

The metacarpals of the Loperot rhinoceros, as shown in Table 16, are not at all as short and wide at mid-shaft as are those of the Chinese *Chilotherium;* the measurements of a set of metacarpals of *Chilotherium anderssoni* as given by Ringström (1924: 58) give the following data for the ratio middle width/length: Mc. II, 0.34; Mc. III, 0.34, and Mc. IV, 0.28. We shall find the same difference in the metatarsals, of which more material of *Chilotherium* is available for comparison. Moreover, in *Chilotherium* the fifth metacarpal is reduced to the same extent as in *Diceros bicornis,* resembling a rounded sesamoid bone about 25 mm in diameter (Ringström, 1924: 57). In a Recent skeleton of this species in the Leiden Museum (Reg. No. 5738) the rudiment of Mc. V is 35 mm long and pointed distally; the proximal facet for the unciform is convex anteroposteriorly and measures 25 by 20 mm in diameter, that for Mc. IV is much smaller, 20 by 7 mm. The fifth metacarpal of the Loperot rhinoceros is small, but has a fully developed distal articular surface. Metacarpal V No. 1 doubtless belonged to the same individual as Mc. IV No. 1, and its median length is three-fifths that of Mc. IV. When the interproximal facets are placed on each other, the Mc. V is seen to be directed backward, its shaft forming an angle of 45° with that of Mc. IV. The proximal end of Mc. V is much extended anteroposteriorly, and bears a large convex facet for the unciform that projects much behind the shaft. The proximal medial facet for Mc. IV is placed along the posterior half of the unciform facet, at right angles to it, and measures only 20 by 10 mm against 30 by 17 mm for the unciform facet. The anterior projection of the proximal end of Mc. V is formed by a protuberance below the unciform facet, which brings the bone on a level with Mc. IV. The shaft of Mc. V, then, diverges distally from that of Mc. IV at an angle of 45°. The distal end of Mc. V with the trochlea is turned outward (away from Mc. IV): the rather asymmetrical trochlea has its median posterior ridge set at an angle of 35° to the anteroposterior long axis of the proximal end. One of the specimens of Mc. V (No. 4) is decidedly longer than the others; unfortunately this specimen cannot be associated with any other metacarpal. In its width/length ratio this bone is within the limits of the three shorter Mc. V Nos. 1–3. Undoubtedly the small Mc. V in the Loperot rhinoceros carried some phalanges, and some of these have been found.

There are very few associations among the metacarpals, but Mc. II No. 2 belonged to the same individual as Mc. III No. 4, and when these bones are held together with their interproximal facets on each other, the Mc. II is seen to be not parallel to Mc. III but directed backward from it at an angle of 15–20°. In the same way, Mc. IV was probably directed backward relative to Mc. III, but there are no associated bones to prove this. The backward divergence of the lateral metacarpals relative to the

TABLE 17. Measurements of metacarpal II in various genera (in mm)

	Brachypotherium	*Chilotherium*	*Diceratherium*	*Chilotheridium*	*Dicerorhinus*
Median length	125	106	122–123	123	136
Proximal width	52	(44)	43–46	41–42	35
Proximal ant. post. diameter	47	39	38–39	36–37	37
Middle width	45	36	34	33	34
Middle ant. post. diameter	25	13	13	15–17	18
Greatest distal width	50	37	33–34	37–43	47
Ratio middle width/length	0.36	0.34	0.28	0.27	0.25

median metacarpal is seen in *Chilotherium* as well (Ringström, 1924: 57). The metacarpals discussed above are presented in Plate 9, figures 4–6.

Of the metacarpals of the Chinese *Diceratherium* only Mc. II is known by entire specimens (Bohlin, 1937: 84). Bohlin gives the greatest length of two Mc. II of *Diceratherium tsaidamense* as 127–129 mm, which makes for a median length of 122 or 123 mm (the greatest length of Mc. II Nos. 1 and 2, both 123 mm in median length, is 129–130 mm). Therefore, the Loperot Mc. II are closely comparable in length to those of *D. tsaidamense*. Bohlin (1937: 85) gives also the dimensions of an Mc. II of *Chilotherium;* the median length of this specimen is only 106 mm by a middle width of 36 mm (Ringström, 1924: 58). In Table 17 the comparisons of Mc. II are extended to include *Brachypotherium heinzelini* Hooijer (1966: 147) from Rusinga, the Mc. II of which, again closely comparable to those of *Diceratherium tsaidamense* in median length, is much more massive at mid-shaft, surpassing *Chilotherium* in this respect. Unfortunately, there are as yet no entire specimens of Mc. II of the African *Aceratherium* or *Dicerorhinus*, but it is conceivable that these would not differ much in proportions from the Mc. II of *Dicerorhinus sumatrensis* (Hooijer, 1966: 166), the measurements of which are given in the last column of Table 17.

Although in the slenderness of the metacarpal the Loperot rhinoceros (*Chilotheridium*) is nearest to *Diceratherium* and *Dicerorhinus*, and far removed from *Chilotherium* and *Brachypotherium* in the peculiar contact of the radius with the cuneiform, not seen in the Recent genera, *Chilotheridium* agrees only with *Chilotherium* and *Diceratherium*. Whether the Chinese *Diceratherium* had an Mc. V is not known; in the American diceratheres it is represented only by a rudiment, as in the living species (Peterson, 1920: 445, pl. LXIII, fig. 1). A small Mc. V, about three-fifths the length of the adjoining Mc. IV, is found in various species of *Aceratherium* (see references in Hooijer, 1966: 153). In a typical *Aceratherium lemanense* of the Aquitanian (Roman, 1924: 52, figs. 23–24) Mc. V is 85 mm long, and Mc. IV 125 mm. In the old illustration of the manus of *Aceratherium tetradactylum* in Duvernoy (1853, pl. VII, fig. 1a), the fifth metacarpal has two phalanges assigned to it, one as wide as the metacarpal itself and squarish, the terminal phalanx narrow and pointed.

Isolated phalanges abound in the Loperot collection, but, with the exception of those of the pes marked 70–64K, B15, 16, they cannot be assigned to any metapodial in particular, and the only categories that can be made are phalanges I, II, and III of either a median or a lateral digit. Some few of the isolated phalanges are decidedly smaller than those of digits II or IV, and these are the ones that I regard as belonging to metacarpal V. The specimens are marked as follows: 1) phalanx I and II (associated), 57–64K; 2) phalanx I, 57–64K; 3) phalanx I, 70–64K; 4)

TABLE 18. Measurements of phalanges of Mc. V from Loperot (in mm)

	No. of specimen						
	1	2	3	4	5	6	7
Phalanx I, length	19	19	21	21	19	18	18
Proximal width	25	24	23	23	21	21	20
Phalanx II, length	14	—	—	—	—	—	11
Proximal width	24	—	—	—	—	—	17

phalanx I, 70–64K, BB; 5) phalanx II, 70–64K, D7; 6) phalanx I, 70–64K, A16; and, 7) phalanx I and II (associated), 70–64K. Measurements are given in Table 18.

Among the rib fragments there is one, marked 70–64K, 65A, preserving the vertebral end and measuring 60 cm along the curve. The greatest width of the rib is *ca.* 50 mm. In the configuration of the head and tubercle it agrees best with the 5th to 7th rib, right side, in Recent skeletons.

The greater part of a left os coxae, marked 70–64K, A16, has the acetabulum and the shaft and most of the wing of the ilium. The specimen is broken into numerous small fragments that have been somewhat forced apart; the spaces between them are filled with plastic and plaster. The ilium is flattened to such an extent that the natural curvations of the gluteal and pelvic surfaces are almost gone. Pubis and ischium are broken off along the borders of the acetabulum, the diameter of which can be given only as 7–8 cm. The naturally three-sided shaft of the ilium is flattened, and measures about 9 cm in least width between the medial and the lateral borders. The concave lateral border of the ilium, up the tuber coxae, is relatively well preserved. Of the anterior border only the convex and thickened lateral half of the iliac crest is there. The tuber sacrale is preserved, but the concave medial border, from there on to the acetabulum, is rather damaged. The diameter of the ilium from acetabulum to the middle of the iliac crest is about 50 cm, and the greatest diameter of the wing from tuber coxae to tuber sacrale is about 55 cm. Both measurements are at least 5 cm too large, considering the filled-in cracks of the bone.

The following specimens of the femur are in the Loperot collection: 1) left femur, 70–64K; 2) left femur, incomplete distally, 70–64K; 3) right femur, immature shaft only, 70–64K, BB; 4) distal epiphysis of right femur, possibly belonging to No. 3, 70–64K; 5) distal end of left femur, 70–64K, A16; and, 6) proximal part of shaft of left femur, 70–64K, BB. Because of the crushing of the specimens very few measurements can be given (Table 19).

The most striking character of the Loperot femora is the small size of the third trochanter. This is shown in No. 1 (Pl. 10, fig. 1) as well as in Nos. 2, 3, and 6. The trochanter tertius is placed just at the middle of the height, is not more than 50 mm vertically at base, and does not project outward and forward for more than 20 mm. The femur of *Dicerorhinus leakeyi* from Rusinga (Hooijer, 1966: 169, pl. 13, fig. 1), 545 mm in greatest length, has a trochanter tertius in the right (unfigured)

TABLE 19. Measurements of femur from Loperot (in mm)

	No. of specimen				
	1	2	3	4	6
Greatest length	*ca.* 470	*ca.* 470	—	—	—
Proximal width	—	*ca.* 180	—	—	—
Width over third trochanter	90	90	75	—	*ca.* 80
Least width of shaft	—	*ca.* 60	55	—	—
Greatest distal width	*ca.* 120	—	—	110	—
Distal ant. post. diameter, medial side	145	—	—	155	—

TABLE 20. Measurements of patella from Loperot (in mm)

	No. of specimen		
	1	2	3
Length	89	89	72
Width	90	93	77

TABLE 21. Measurements of tibia from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Greatest length	320	*ca.* 360	—	—
Medial length	285	*ca.* 320	—	—
Proximal width	118	—	—	—
Middle width	45	*ca.* 55	—	—
Distal width	88	95	93	96
Distal ant. post. diameter	69	*ca.* 75	—	71

specimen that measures 100 mm high vertically at its base and projects outward and forward, extending the width across this process to 130 mm in contrast to the least width of the shaft below it of 75 mm. In Recent *D. sumatrensis* the third trochanter is likewise well developed; a femur not very much shorter than the Loperot specimens (greatest length 423 mm) has a width over the third trochanter of 115 mm by a least shaft width of 56 mm. The femora of *Chilotherium* do show a large and prominent third trochanter; Ringström (1924: 62, pl. IX, fig. 4) figures a specimen of *Chilotherium* from China only 430 mm in greatest length but with a width over the third trochanter of 128 mm, and a least width of shaft (estimated) of *ca.* 60 mm, while the *Chilotherium* femur from the Middle Siwaliks figured by Colbert (1935: 211, fig. 96) is likewise twice as wide over the third trochanter as its least shaft width.

It is in *Diceratherium tsaidamense* that we find a third trochanter on the femur that is just as small as that in the Loperot rhinoceros (Bohlin, 1937: 87, pl. IX, fig. 4); the width over the third trochanter is only one-half greater than the least shaft width. However, in the other Chinese *Diceratherium*, *D. palaeosinense*, the femur is nearer to that of *Chilotherium*, and its third trochanter is even somewhat larger than that in the latter genus (Bohlin, 1937: 87).

Of the patella there are three entire specimens in the Loperot collection as well as parts of five others. Number 1 is a right patella, 70–64K; No. 2 a right patella, 57–64K; No. 3 a left patella, 70–64K, E10; whereas the fragments come from 70–64K, D11 (surface), D12, and BB. The Loperot patellae are slightly wider than long (Table 20), the Rusinga patellae longer than wide (Hooijer, 1966: 170), but this difference is most probably insignificant. A patella of *Chilotherium anderssoni* (Ringström, 1924: 58) is 90 mm long and 87 mm wide; a specimen of *Diceratherium tsaidamense* (Bohlin, 1937: 88) measures 79 mm in length.

The following specimens of the tibia are in the Loperot collection: 1) right tibia, 70–64K, A16; 2) right tibia, damaged at both ends, 70–64K; 3) right tibia, proximal part flattened, 70–64, BB; 4) distal end of right tibia, 57–64K; 5) proximal end of shaft of left tibia, 70–64K, BB?; and, 6) lateral distal fragment of left tibia, 70–64K, E10. Measurements (Table 21) show that the most complete specimen is the smallest; yet it is longer than the tibia in *Chilotherium* by the same middle and distal widths (Ringström, 1924: 58 and 63; length 275–*ca.* 280 mm, middle width 47–48 mm, distal width 84–86 mm). The greatest length of the Middle Siwalik *Chilotherium* tibia is only 245 mm by a middle width of 43 mm (Colbert, 1935: 212).

The difference between proximal and distal width is less in *Chilotherium* (105 and 92 mm, respectively) than in *Diceratherium tsaidamense* (95 and 69 mm, respectively); in the latter species (measurements taken from Bohlin, 1937: 89) the proximal width is one-third greater than the distal width,

TABLE 22. Measurements of fibula from Loperot (in mm)

	No. of specimen					
	1	2	3	5	6	7
Length	290	*ca.* 300	255	—	—	—
Greatest proximal diameter	44	45	40	—	—	—
Mid-shaft diameters	21 × 14	—	19 × 14	—	—	—
Greatest distal diameter	48	—	41	45	38	38

as it is in Loperot tibia No. 1 (see Pl. 10, fig. 2).

Although there are seven specimens of the fibula in the Loperot collection none of these appears to belong to any of the tibiae. Nor is there any case of ankylosis of these bones, in contradistinction to what we find in *Chilotherium* (Ringström, 1924: 58). The specimens are as follows: 1) right fibula, 70–64K, 65C; 2) left fibula, 70–64K, 65C; 3) right fibula, 70–64K, B15, 16; 4) proximal portion of right fibula, 70–64K; 5) distal end of left fibula, 70–64K; 6) distal end of right fibula, 70–64K; and, 7) distal end of left fibula, 70–64K.

Bohlin (1937: 89) found a fibula of *Diceratherium tsaidamense* to be more rounded in section at mid-shaft (17 × 17 mm) than one of *Chilotherium* (24 × 14 mm). If this is a good distinguishing character the Loperot bones are closer to *Chilotherium* than to *Diceratherium* (Table 22). The best preserved Loperot fibula is figured in Plate 10, figure 3.

There is most of a right pes in the Loperot collection; all bones are marked 70–64K, B15, 16, and fit together so well that there is no doubt as to their belonging to a single individual. There are the astragalus, calcaneum, navicular, cuboid, ectocuneiform, and all three metatarsals with their three phalanges each except for the third phalanx of the fourth digit; there is even one sesamoid. Thus, the tarsals missing are the mesocuneiform and the entocuneiform, but of these there are several specimens of other individuals in the collection. The bones in this right pes (Pl. 10, fig. 4) are all No. 1 in their series.

The series of Loperot astragali is as follows: 1) right astragalus, 70–64K, B15, 16; 2) right astragalus, 70–64K; 3) right astragalus, 70–64K, A16, 17; 4) left astragalus, 70–64K, A18; and, 5) left astragalus, 70–64K, C12. Numbers 2–5 are incomplete distally. In addition there are seven fragments of right, and four fragments of left astragali; of these no measurements can be given.

In the Loperot astragali (Table 23) the ratio of medial height to total width (0.72–0.77) is intermediate between that in *Brachypotherium* (0.64–0.73) on the one hand and that in *Dicerorhinus* and *Aceratherium* (0.80–0.97) on the other (Hooijer, 1966: 148 and 173). The trochlea width is slightly greater than the medial height, as may be the case in *Dicerorhinus* and *Aceratherium* (Hooijer, 1966: 174); in *Brachypotherium* the difference between these two measurements is greater. Ringström (1924: 58) mentions that in a large number of entire *Chilotherium* astragali the three calcaneum facets are separate, whereas in the astragalus of *Diceratherium* (Ringström, 1924: 111) the medial and the distal

TABLE 23. Measurements of astragalus from Loperot (in mm)

	No. of specimen				
	1	2	3	4	5
Lateral height	65	71	—	72	63
Medial height	65	—	64	72	67
Total width	89	—	89	93	89
Ratio medial height/total width	0.73	—	0.72	0.77	0.75
Trochlea width	70	75	67	76	71
Width of distal facets	73	—	—	79	73

TABLE 24. Measurements of calcaneum from Loperot (in mm)

	No. of specimen									
	1	2	3	4	5	6	7	8	9	10
Lateral height	112	126	132	—	—	113	—	—	—	—
Greatest width	74	—	*ca.* 75	—	—	68	—	—	—	—
Ratio width/height	0.66	—	*ca.* 0.57	—	—	0.60	—	—	—	—
Ant. post. diam. cuboid facet	42	—	40	—	—	42	—	—	—	—
Transverse diam. of same	25	—	22	—	21	22	—	—	—	—
Greatest diameter of tuber	59	62	72	61	59	70	—	59	*ca.* 60	51
Transverse diam. of same	42	42	48	40	45	43	47	42	41	40

calcaneum facets are confluent. I do not consider this difference to be of any significance (cf. Hooijer, 1966: 174, footnote). As follows from Ringström's illustrations the astragalus of *Diceratherium* is relatively higher than that of *Chilotherium;* measurements are given only by Bohlin (1946: 228), and they show that in *Diceratherium palaeosinense* the medial height exceeds the trochlea width, whereas in *Chilotherium* the trochlea width slightly exceeds the medial height. Both conditions are found in *Dicerorhinus* and *Aceratherium.* The total width of the *Chilotherium* and *Diceratherium* astragali is not recorded, but I have measured an astragalus of the Middle Siwalik *Chilotherium* recorded by Colbert (1935: 212) and found the medial height to be 60 mm and the total width 77 mm, giving a ratio of 0.78, very much as in the Loperot astragali and in those of *Dicerorhinus* and *Aceratherium.* It is clear that not only are the Loperot astragali not as much shortened as in *Brachypotherium* but they are also not as long as in *Dicerorhinus* and *Acertherium* on the whole; they are nearer to *Chilotherium* than to *Diceratherium* in that the trochlea width slightly exceeds the medial height, admittedly a variable feature. The relative height of the Loperot astragali is more like that in *Chilotherium* than in *Diceratherium* (cf. Ringström, 1924: text-figs. 40 and 71–72), the approximate medial height/total width ratio as taken from the figures being 0.75 in the former against 0.81 in the latter.

The calcaneum is again well represented in the collection from Loperot, although in the majority of the specimens the transverse process, the sustentaculum tali, has broken off, and the proximal portion with the cuboid facet is missing in one-half the number of specimens (Nos. 4 and 7–10). In No. 1 the sustentaculum tali is preserved separately and there has been some loss of substance so that it does not fit on to the remainder of the calcaneum, but the associated astragalus fits the calcaneum so perfectly that the greatest width can nevertheless be taken. The series is as follows: 1) right calcaneum, 70–64K, B15, 16; 2) right calcaneum, 70–64K, BL; 3) right calcaneum, 70–64K, A18; 4) right calcaneum, 70–64K, A16, 17; 5) right calcaneum, 68–64K, tuber portion and proximal portion separate; 6) left calcaneum, 70–64K, BB; 7) left calcaneum, 70–64K, A16; 8) left calcaneum, 70–64K, E10; 9) left calcaneum, 70–64K, E12; and, 10) left calcaneum, 70–64K.

The calcaneum of *Chilotherium* is rather short and massive (Ringström, 1924: 58, pl. VIII, fig. 7), and has the three astragalar facets separate, whereas in *Diceratherium palaeosinense* the two lower astragalar facets are confluent. In the few Loperot calcanea in which this can be checked there is no fusion of the two lower facets for the astragalus (and neither is there any fusion of the two corresponding facets for the calcaneum on the astragali of Loperot). This feature is variable in *Diceratherium* (Bohlin, 1937: 89), and is evidently not a very reliable character. In the Loperot

TABLE 25. Measurements of navicular from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Greatest anterior height	22	20	19	*ca.* 19
Total width	49	50	*ca.* 50	—
Ant. post. diameter	61	—	63	—

astragali there is no trace of a facet for the tibia behind and lateral to the upper facet for the astragalus; this facet is mentioned by Bohlin as most characteristic of *Chilotherium*. There remains a slight difference in relative height of the calcaneum: in the Loperot calcanea (Table 24) the ratio width/length is *ca.* 0.57–0.66, while in two *Chilotherium* calcanea this ratio is 0.67 and 0.74, but in four specimens of *Diceratherium tsaidamense* and *D. palaeosinense* the width/length ratio is 0.61–0.71 (cf. Bohlin, 1937: 90). The development of the tuber calcanei is too variable to be of any value for specific distinction. Thus, the Loperot calcanea are slightly longer than those in *Chilotherium*, but differ in not having a facet for the tibia; on the whole they are nearer to *Diceratherium* from China.

The navicular of the right pes from 70–64K, B15, 16, is not complete; it has a cut in the anterior face and lacks a portion posterolaterally. The other naviculars are not complete either. The series is: 1) right navicular, 70–64K, B15, 16; 2) right navicular, incomplete posteromedially, 57–64K; 3) right navicular, lacking the posterolateral portion, 70–64K; and, 4) left navicular, all borders except the lateral incomplete, 70–64K, C11. In *Chilotherium andersoni* this bone (called Centrale) is wider behind than in front; it has an obtuse anteromedial angle (Bohlin, 1937: 90, fig. 155). That of *Diceratherium tsaidamense* (Bohlin, 1937: 90, fig. 156) is not as wide behind and is more nearly rectangular (it should be noted that in the upper [proximal] views of the navicular given by Bohlin [1937: figs. 155 and 156] the anterior side is above, and the medial to the right). Our Loperot naviculars (Table 25) are decidedly more rectangular than is that of *Chilotherium* (the width of the latter, given as 59 mm by Ringström [1924: 60], as Bohlin's figure 155 shows, is only 50 mm behind and 30 mm in front), and agree with the navicular in *Diceratherium tsaidamense* in that anteroposterior diameters are about one-fifth greater than the width (46 mm, and 38 mm); in *Chilotherium* the anteroposterior diameter is very nearly equal to the (posterior) width (52 mm, and 53 mm: Bohlin, 1937: 90).

There are two facets for the cuboid laterally on the navicular, a small and low anterior one, and a larger posterior facet that is not vertical but oblique, facing downward and outward. Between these two facets there is a nonarticular groove or fossa. We find, of course, the corresponding facets on the cuboid, the posterior facet facing upward and inward. The latter facet is bordered below by a nearly vertical facet that articulates with the ectocuneiform, for which there is also an anterior medial facet on the cuboid, placed below the anterior navicular facet and separated from it by a nonarticular groove. A third element that articulates with the medial surface of the cuboid is metatarsal III, situated, of course, below the ectocuneiform: there is a very small but yet distinct facet proximally and anteriorly on the lateral surface of metatarsal III, placed between the large proximal ectocuneiform facet and the anterior of the two lateral metatarsal IV facets. On the cuboid itself this little facet is practically indistinguishable; in the articulated pes, the cuboid facet on metatarsal III forms just a small downward extension of the cuboid facet on the ectocuneiform.

The relations of the contact facets between cuboid on the one hand, and navicular, ectocuneiform, and metatarsal III on the other, described in the preceding paragraph, exist in the Loperot rhinoceros and

TABLE 26. Measurements of cuboid from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Anterior height	32	35	32	35
Anterior width	41	41	36	39
Greatest ant. post. diameter	60	63	—	56

in Recent *Diceros bicornis* and *Dicerorhinus* (Recent and fossil) as well. Admittedly the facet for the third metatarsal on the cuboid is hardly discernible, but when the associated metatarsal III is examined, we find the little cuboid facet, which truncates the edge between the ectocuneiform facet and the metatarsal IV facet on the middle metatarsal. In *Dicerorhinus sumatrensis* as well as in both *Dicerorhinus leakeyi* (Hooijer, 1966: pl. 13, fig. 3) and *Diceros bicornis* there is a contact between cuboid and metatarsal III as well as a contact between cuboid and ectocuneiform. I am mentioning this specially because Ringström (1924: 59) states that in the Recent forms there is a distinct facet on the cuboid (Tarsale IV & V) for metatarsal III, but none or only a very indistinct one for the ectocuneiform (Tarsale III). This is not in accord with my own observations; on the contrary, the ectocuneiform facets are much more clearly seen than the metatarsal III facets. This reverse situation is the one that obtains in *Chilotherium;* Ringström states that in that genus the ectocuneiform facet on the cuboid is large, whereas there is no metatarsal III facet on the cuboid. As far as I know this is the condition in the nonchilothere rhinoceroses as well, and no reliance can be placed on this for the distinction between genera.

Ringström (1924: 59) further mentions that in *Chilotherium* the two proximal facets for astragalus and calcaneum meet at an obtuse angle in the middle of the cuboid and are separated by a ridge, a condition elsewhere found only in *Teleoceras.* The obtuse angle and a smooth ridge (not a very sharp one) is seen in the Recent forms as well as in the Loperot cuboids. Of these cuboids we have four specimens, as follows: 1) right cuboid, 70–64K, B15, 16; 2) right cuboid, 70–64K, D11; 3) right cuboid, incomplete behind, 70–64K; and, 4) right cuboid, idem, 70–64K, A16, 17. The measurements are given in Table 26.

All four of the Loperot cuboids are wider than high anteriorly; this is, however, much more marked in the cuboid of *Chilotherium anderssoni,* with a height of 27 mm and a width of 46 mm (Ringström, 1924: 60). The great width in the Loperot cuboids, it seems, is caused by the presence of a lateral outgrowth of bone that is well separated from the proximal (calcaneum) and distal (metatarsal IV) facets. This outgrowth is a very distinctive feature of the Loperot specimens, and does not show in the cuboids of *Dicerorhinus* and *Aceratherium* (Hooijer, 1966: 176, pl. 13, figs. 5 and 6). In the cuboids of these two genera anterior height and width are either nearly equal, or the height exceeds the width. The cuboid of *Chilotherium* is seen to project laterally much beyond the fourth metatarsal (Ringström, 1924: pl. IX, fig. 3); it does not do so in the Loperot rhinoceros as the articulated pes (Pl. 10, fig. 4) shows. Unfortunately there is no cuboid of the Chinese *Diceratherium* on record.

Five ectocuneiforms are in the Loperot collection: 1) right ectocuneiform, 70–63K, B15, 16; 2) right ectocuneiform, 70–64K; 3) right ectocuneiform, 70–64K, A16; 4) left ectocuneiform, 70–64K, incomplete medially; and, 5) left ectocuneiform, 70–64K, D11. This bone, the cuboid facets of which have already been mentioned, has two medial proximal facets for metatarsal II, and a small, high-placed posterior medial facet for the mesocuneiform. The width anteriorly is very nearly twice the anterior height (Table 27), in which it contrasts with the ectocuneiform of *Chilotherium,* with a width (44 mm) nearly

TABLE 27. Measurements of ectocuneiform from Loperot (in mm)

	No. of specimen				
	1	2	3	4	5
Anterior height	21	23	21	21	23
Anterior width	42	44	43	—	45
Ant. post. diameter	44	48	46	43	48

TABLE 28. Measurements of mesocuneiform from Loperot (in mm)

	No. of specimen		
	1	2	3
Height	13	12	15
Width	21	20	22
Anteroposterior diameter	32	33	34

three times the height (15 mm) (Ringström, 1924: 60). The ectocuneiform of the Chinese *Diceratherium* has not been described.

The mesocuneiform, a bone missing in the right pes from 70–64K, B15, 16, fits on to metatarsal II and has a correspondingly shaped distal facet, transversely convex anteriorly, elongated anteroposteriorly, ending narrow behind. There are three specimens: 1) right mesocuneiform, 68–64K; 2) right mesocuneiform, 70–64K, D11; and, 3) left mesocuneiform, 70–64K. The bone has a facet for the ectocuneiform proximally on the lateral side, and another one for the entocuneiform posteromedially. The latter facet is either limited to the proximal part and is then continuous with the entocuneiform facet on the navicular, or the facet on the mesocuneiform may extend along the full height and, in that case, it is continuous with both the facet on the navicular and that on metatarsal II. The first-mentioned condition is seen in mesocuneiforms 1 and 3, whereas the second condition obtains in mesocuneiform 2. The entocuneiform facets on mesocuneiforms 1 and 3 differ much in size. Although No. 3 is larger than No. 1, the entocuneiform facet is smaller in No. 3, in which it is confined to the proximal third of the height, than in No. 1, in which it occupies the proximal half of the height. The measurements (Table 28) indicate that the Loperot mesocuneiforms are not as wide relative to their height as the mesocuneiform of *Chilotherium*, which has a height of 12 mm by a width of 23 mm (Ringström, 1924: 60: Tarsale II). The difference is rather small.

Of the entocuneiform we have three specimens in the Loperot collection: 1) right entocuneiform, 70–64K; 2) left entocuneiform, 70–64K, D11; and, 3) left entocuneiform, 70–64K. The posterior tuberosity is missing in the last specimen. This bone, which is placed behind the mesocuneiform, has a large, nearly horizontal facet proximally for the navicular. At right angles to it (nearly vertical) is a small facet for the mesocuneiform, which may, or may not, be continuous with the facet for metatarsal II. Ringström (1924: 59) and Bohlin (1937: 90), who refer to the entocuneiform as the large sesamoid bone, mention these three facets in *Chilotherium anderssoni* and *Diceratherium tsaidamense* but do not mention whether the mesocuneiform and metatarsal II facets are separate or united. In Loperot No. 1 these two facets are continuous, but in Nos. 2 and 3 the facets for mesocuneiform and metatarsal II are separated by a nonarticular fossa (among the mesocuneiforms treated above the same variation occurs, No. 2 showing the entocuneiform facet to be continuous with that on metatarsal II, Nos. 1 and 3 showing these to be separate). The proximal facet for the navicular is the largest of all facets, the facet for the mesocuneiform is low and wide, and only in entocuneiform No. 1 it is continuous with the vertical, narrow facet for metatarsal II. In Table 29 I give the measurements of the Loperot specimens as well as those of *Chilotherium* and *Diceratherium* of China; the anteroposterior diameter (width in the table of Bohlin, 1937: 90) is taken above, thus not including the posterior hook-

TABLE 29. Measurements of entocuneiform from Loperot (in mm)

	No. of specimen 1	2	3	*Chilotherium*	*Diceratherium*
Height	42	43	31	50	40
Anteroposterior diameter	33	31	29	32	26
Width	18	17	14	15	18

shaped process, and the width (thickness in Bohlin's table) is transverse.

The variability in the Loperot series is so great as to make the intergeneric differences in size and proportions appear meaningless; lateral views of Loperot Nos. 1 and 2 are given in Plate 9, figures 1–2.

Apart from the right Mt. II–IV of the associated pes there are only two entire metatarsals, and, further, some proxima

TABLE 30. Measurements of metatarsals II–IV from Loperot (in mm)

Mt. II	No. of specimen 1	2	3	*Chilotherium* Siwaliks
Median length	110	119	—	94
Proximal width	28	31	*ca.* 24	*ca.* 23
Proximal ant. post. diameter	39	—	—	*ca.* 33
Middle width	23	27	—	23
Middle ant. post. diameter	21	26	—	18
Greatest distal width	35	42	—	*ca.* 30
Width of distal trochlea	34	38	—	*ca.* 26
Distal ant. post. diameter	38	43	—	32
Ratio middle width/length	0.21	0.23		0.24

Mt. III	No. of specimen 1	
Median length	124	104
Proximal width	43	41
Proximal ant. post. diameter	40	*ca.* 40
Middle width	37	34
Middle ant. post. diameter	19	*ca.* 18
Greatest distal width	49	44
Width of distal trochlea	43	39
Distal ant. post. diameter	36	—
Ratio middle width/length	0.30	0.33

Mt. IV	No. of specimen 1	2	3	4	
Median length	109	107	—	—	87
Proximal width	39	39	41	44	*ca.* 37
Proximal ant. post. diameter	*ca.* 40	43	—	—	41
Middle width	23	22	—	—	24
Middle ant. post. diameter	21	21	—	—	16
Greatest distal width	33	34	—	—	—
Width of distal trochlea	33	35	—	—	*ca.* 28
Distal ant. post. diameter	36	35	—	—	—
Ratio middle width/length	0.21	0.21	—	—	0.28

Table 31. Measurements of metatarsal IV in various species (in mm)

	Chilotherium anderssoni	*Diceratherium palaeosinense*	*Diceratherium tsaidamense*	*Chilotheridium pattersoni*	*Dicerorhinus leakeyi*
Median length	89–90	83	—	107–109	166
Proximal width	36–37	34	29	39	44
Proximal ant. post. diameter	39	41	31	*ca.* 40–43	46
Middle width	25	29	20	22–23	29
Middle ant. post. diameter	—	—	—	21	—
Greatest distal width	—	—	—	33–34	38
Ratio middle width/length	0.28	0.35	—	0.21	0.18

portions of metatarsals in the Loperot collection, as follows:

Metatarsal II, 3 specimens: 1) right Mt. II, 70–64K, B15, 16; 2) right Mt. II, damaged proximally, 70–64K, BB; and, 3) right Mt. II, proximal portion only, 70–64K.

Metatarsal III, 1 specimen: 1) right Mt. III, 70–64K, B15, 16.

Metatarsal IV, 5 specimens: 1) right Mt. IV, damaged proximally, 70–64K, B15, 16; 2) left Mt. IV, 70–64K, 65B; 3) left Mt. IV, proximal portion, incomplete behind, 70–64K, D11; 4) left Mt. IV, proximal portion, incomplete medially, 70–64K, A16, 17; and, 5) right Mt. IV, proximal end, incomplete anteriorly and laterally, 70–64K, D12.

When the measurements and indices of the Loperot metatarsals are compared with those of *Paradiceros mukirii* of Fort Ternan (Hooijer, 1968b: 87), it is seen that the Loperot Mt. II is nearly identical with that of Fort Ternan, and that the single Loperot Mt. III is perfectly intermediate between the two Mt. III of *Paradiceros mukirii* on record. I found the same to be true for Mc. III. Yet the two forms are widely different cranially and dentally (above, p. 340).

The metatarsals from Loperot are longer and relatively more slender than those of *Chilotherium;* the measurements in the last column of Table 30 are those of the pes from the Middle Siwaliks recorded by Colbert (1935: 212) and taken by me on a visit to the American Museum of Natural History in New York in September 1965. The difference in relative length is greatest in metatarsal IV. The metatarsals of *Chilotherium anderssoni,* the length and middle width of which are given by Ringström (1924: 60), are very similar to those of the Middle Siwalik *Chilotherium:* Mt. II, 24–25 mm; Mt. III, 36–37 mm, and Mt. IV, 27–29 mm. As already mentioned above, the Loperot Mt. III has a small cuboid facet; according to Ringström (1924: 72) *Chilotherium* does not have a cuboid facet on its metatarsal III.

According to measurements recorded by Bohlin (1937: 91), metatarsal IV of the Chinese *Chilotherium* (two specimens) has a middle width/length ratio of 0.28, but that of *Diceratherium palaeosinense* is incomplete but seems to be much slenderer. The measurements are given in Table 31, together with those of the Loperot *Chilotheridium* and those of *Dicerorhinus leakeyi* (Hooijer, 1966: 179), which has the slenderest shaft of all Mt. IV recorded here.

Metatarsal IV of the Loperot species is nearest to *Dicerorhinus* in relative shaft width (in Recent *D. sumatrensis* the ratio is 0.20). The proximal facet (for the cuboid) is almost flat, as it is in *Chilotherium* as well as in *Diceratherium palaeosinense;* in *D. tsaidamense* (according to the incomplete specimen referred to this species by Bohlin, 1937: 91, figs. 159 and 160) the cuboid facet is raised laterally, and, further, the posterior of the two facets for metatarsal III is placed lower than the anterior. In the Loperot form the posterior metatarsal II facet is placed slightly lower than the anterior, as in fossil

TABLE 32. A. Distal ends of median metapodials from Loperot (in mm)

No.		Greatest width	Trochlea width	Ant. post. diameter
1	70–64K, E10	59	48	—
2	70–64K, B16	47	43	37
4	70–64K	*ca.* 54	48	—
5	70–64K	—	—	44
6	68–64K	—	43	—
7	70–64K, A16, 17	52	—	39
8	70–64K, D11	—	43	36
	B. Distal ends of lateral metapodials			
1	57–64K	42	37	37
3	70–64K	48	38	39
4	70–64K, BB	42	38	—
5	70–64K	46	35	36
6	70–64K	—	*ca.* 30	35
7	70–64K	45	38	—
8	57–64K	38	37	38
9	70–64K	—	32	36
10	70–64K	36	34	39
11	70–64K	40	35	—
12	70–64K, A16, 17	30	31	—
13	70–64K	41	35	41
14	70–64K	—	35	—
15	70–64K, D11	—	31	38
16	70-64K, D11	33	33	—

TABLE 33. Measurements of posterior phalanges from Loperot (in mm)

	Digit		
	II	III	IV
Phalanx I, length	30	31	30
Proximal width	34	45	32
Phalanx II, length	22	20	18
Proximal width	33	42	31
Phalanx III, length	34	31	—
Greatest diameter	45+	70	—

and Recent *Dicerorhinus*. In the articulated pes (70–64K, B15, 16) there is only a slight posterior divergence of the lateral metatarsals relative to the median; this is more marked in *Chilotherium* (Ringström, 1924: 60, pl. IX, fig. 3). What the position of the lateral metatarsals in the Chinese *Diceratherium* is I do not know.

As seen in the proximal views of Mt. IV of *D. tsaidamense* and *Chilotherium* (Bohlin, 1937: 91, figs. 159 and 161), the bone extends laterally beyond the cuboid facet, which is sharply marked off laterally. Such a collar of bone is also found lateral to the proximal cuboid facet in the Loperot specimens; it is particularly well developed in No. 3 (Pl. 9, fig. 3), which is from the left side as are Bohlin's specimens. In the articulated pes this bone prominence is placed just below the lateral bone development on the cuboid, serving for attachment of ligaments. We do not find such a development in Recent *Dicerorhinus*, and in *D. leakeyi* it is present, but placed posteriorly rather than laterally.

Measurements of a number of distal ends of median as well as of lateral metapodials are given below.

The phalanges I–III of digits II and III, and phalanges I and II of digit IV of the right pes (70–64K, B15, 16) are available, and their measurements are given in Table 33.

The measurements of the first phalanx of digit III agree very well with those in *Diceratherium tsaidamense* (length 29 mm, width 45 mm: Bohlin, 1937: 86), and those of the first phalanx of digit II are the same as those in this species as well as in *Chilotherium* (length 30 mm, width 34 mm: Bohlin, 1937: 85). In *Brachypotherium heinzelini* the proximal phalanges of these digits are shorter and wider (length 28 mm, proximal width 55 mm in digit III, and length 28 mm, proximal width 43 mm in a lateral digit: Hooijer, 1966: 149), while in *Dicerorhinus leakeyi* the proximal phalanges of these digits are much longer (length 40 mm, proximal width 55 mm in digit III, and length 37 mm, proximal width 40 mm in digit II: Hooijer, 1966: 180).

There remain a fair number of isolated phalanges in the Loperot collection; whether they belong to the fore or to the hind foot is impossible to tell. These specimens are enumerated below.

Of the third phalanges of the median digit only one specimen is entire (70–64K, BB?). It is 31 mm high and the greatest

TABLE 34. Phalanx 1, median digit from Loperot (in mm)

No.		Length	Proximal width
1	70–64K, E10	29	50
2	70–64K	33	49
3	70–64K	30	46
4	70–64K	31	47
5	68–64K	31	48
6	70–64K, BB	29	51
7	68–64K	31	49
8	70–64K	33	46
9	70–64K, A16, 17	33	43
10	70–64K	31	41
11	70–64K, A16, 17	31	43
12	68–64K	31	45
13	57–64K	28	52
14	57–64K	30	49
15	70–64K	29	42
	Phalanx 2, median digit		
1	70–64K, E12	24	49
2	57–64K	20	52
3	70–64K, A16	19	53
4	70–64K	20	43
5	70–64K	21	43
6	70–64K	19	49
7	70–64K	21	*ca.* 53
8	70–64K, A16, 17	20	44
9	68–64K	21	*ca.* 55
10	70–64K, EM	21	48
11	57–64K	23	49

Phalanx 1, lateral digit

No.		Length	Proximal width
1	70–64K, E10	31	37
2	70–64K, A17	30	*ca.* 33
3	70–64K	32	38
4	70–64K, A16	32	34
5	57–64K	30	40
6	70–64K, BB	32	39
7	70–64K	32	36
8	70–64K, H10	30	33
9	70–64K	31	34
10	57–64K	29	34
11	70–64K	28	30
12	70–64K	33	41
13	70–64K	30	32
14	70–64K	30	35
15	70–64K	31	35
16	57–64K	28	37
17	70–64K, B14	30	33
18	70–64K, D11	30	37
19	70–64K	29	33

TABLE 34. (Continued)

Phalanx 2, lateral digit

1	70–64K	21	37
2	70–64K, D11	20	33
3	70–64K, D11	20	34
4	70–64K, D12	21	39
5	70–64K	22	32
6	70–64K, A16, 17	21	34
7	70–64K, A16, 17	18	37
8	70–64K	28	41
9	57–64K	19	35
10	70–64K, H11	20	37
11	70–64K	20	32
12	70–64K	20	34
13	57–64K	21	41
14	70–64K, B14	18	30
15	57–64K	19	41
16	68–64K	19	33
17	70–64K, A16, 17	21	34
18	70–64K	19	32

(transverse) diameter is 78 mm. Of the third phalanges of lateral digits there are only incomplete specimens varying in greatest length from 33 to 41 mm; the transverse diameter cannot be taken in any of the specimens. These terminal phalanges, which belong either to digit II or to digit IV, manus or pes, are as rough and porous, with many perforations on or near the distal border, as the end phalanges of digit III. I find this also in the living rhinoceroses. Ringström (1924: 63) found the terminal phalanx of a lateral digit of *Chilotherium* to be much less rough on the surface, with few, small perforations showing, and states that this is probably because the lateral digits diverge backward and are functional only to a very slight extent.

To round off the account of the remains of the Loperot rhinoceros I have to mention the sesamoid bones. One, a proximal sesamoid of the median digit, is associated with the right pes marked 70–64K, B15, 16; there are eleven more sesamoids of digit III (manus or pes), and there are twenty entire proximal sesamoids of lateral digits (II or IV), as listed below.

TABLE 35. Proximal sesamoids from Loperot (in mm)

No.		Length	Width
	median digit		
1	70–64K, B15, 16	38	19
2	57–64K	46	24
3	70–64K, A16	38	18
4	70–64K	45	22
5	57–64K	37	19
6	70–64K	43	22
7	70–64K	45	24
8	57–64K	48	22
9	70–64K	39	18
10	70–64K	41	21
11	70–64K	40	21
12	70–64K	41	22
	lateral digit		
1	70–64K, D11	35	18
2	70–64K	36	18
3	70–64K, A16	31	15
4	70–64K	35	19
5	70–64K	32	16
6	70–64K, D11	27	15
7	70–64K	34	17
8	70–64K	27	16
9	70–64K	33	17
10	70–64K	31	15
11	57–64K	34	18
12	70–64K	31	16
13	70–64K	34	17
14	70–64K	29	15
15	70–64K	29	14
16	70–64K	30	16
17	70–64K	32	15
18	70–64K	29	16
19	70–64K	32	17
20	70–64K	34	16

TABLE 36. Distinguishing characters of *Chilotherium*, *Chilotheridium*, and *Diceratherium*[1]

Chilotherium	Chilotheridium	Diceratherium
Hornless in both sexes	Small single nasal horn in both sexes	Small terminal nasal pair of horns (♂) or hornless (♀)
Frontals and parietals not pneumatized	Frontals and parietals pneumatized	Frontals and parietals pneumatized
Orbit placed very high, just below upper skull contour	Orbit not placed so very high	Orbit not placed so very high
Cranium and occiput not narrowed	Cranium and occiput rather narrow	Cranium and occiput rather narrow
Parietal crests widely separated	Parietal crests not widely separated	Parietal crests not widely separated
Inferior squamosal processes not united below	Inferior squamosal processes not united below	Inferior squamosal processes united below
Mandibular symphysis much widened anteriorly	Mandibular symphysis narrow, slightly expanded anteriorly	Mandibular symphysis narrow, not widening to the front
Lower C widely separated	Lower C not so widely separated	Lower C not so widely separated
Cheek teeth hypsodont	Cheek teeth hypsodont	Cheek teeth subhypsodont
Scapula high and slender	Scapula low and wide	Scapula low and wide
Humerus, radius, femur, and tibia shortened	Humerus, radius, femur, and tibia not much shortened	Humerus, radius, femur, and tibia not much shortened

Table 36. (Continued)

Ulna ankylosed with radius	Ulna not united with radius	Ulna not united with radius
Fibula ankylosed with tibia, and not rounded in mid-shaft section	Fibula not united with tibia, and not rounded in mid-shaft section	Fibula not united with tibia, and rounded in mid-shaft section
Femur with large third trochanter	Femur with small third trochanter	Femur (in _D. tsaidamense_ only) with small third trochanter
Manus and pes tridactyl	Manus tetradactyl, pes tridactyl	Manus probably tridactyl, pes tridactyl
Astragalus moderately long	Astragalus moderately long	Astragalus longer
Calcaneum short, with facet for tibia behind upper facet for astragalus	Calcaneum somewhat longer, without tibia facet	Calcaneum somewhat longer, without tibia facet
Navicular wider behind than in front	Navicular nearly rectangular	Navicular nearly rectangular
Cuboid much wider than high, ridged between astragalus and calcaneum facets	Cuboid wider than high, with lateral bone prominence, smooth ridge between astragalus and calcaneum facets	(Cuboid unknown)
Metapodials short, lateral metapodials diverging posteriorly	Metapodials longer, lateral metapodials somewhat divergent posteriorly	Metapodials longer, but (in _D. palaeosinense_) Mt. IV rather short
Metatarsal III without facet for cuboid	Metatarsal III with small facet for cuboid	(Metatarsal III unknown)

[1] The three genera agree in the following characters: premaxillaries weak, no upper I, radius with cuneiform facet, and lunar without facet for the ulna.

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APPENDIX

Hypodigm of *Chilotheridium pattersoni* Hooijer, gen. et sp. nov.

Field No. 70–64K, found by B. Patterson.

Skull, C9–10	(No. 1)
" , TYPE, B12	" 2
Right and left maxilla, 65B	
Nasal bones, A″18	
M^3, right, C9–10	
Mandible	(No. 1)
" , 65	" 2
" , B11	" 3
" , right ramus, part of left, 65C	" 4
" , part of left ramus, A18	" 5
Lower canine, left, 65	
" " , right, A16	
Atlas, 65B	
" , C1	
Left scapula, A18	
Right " , BB	
" " , BL	
" " , 65B	
" " , BB	
Right humerus, A18	(No. 1)
" " , BB	" 2
" " , —	" 3
" " , distal end, —	" 4
Right radius, BB	(No. 1)
Left " , A16	" 2
Right " , C14	" 3
Left " , C14	" 4
Right " , BB	" 5
Left " , A17	" 6
Right " , BB	" 7
" " , proximal end, —	" 8
" " , " " , E10	" 9
" " , distal end, —	" 10
" " , " " , B16	" 11
" " , " " , C12	" 13
Left " , " " , BB	" 14
Right " , " " , —	" 15
Left ulna, A17	(No. 1)
Right " , —	" 2
" " , BB	" 3
" " , BB	" 4
Left " , C14	" 5
" " , C14	" 6
" " , BB	" 7
Right " , A17	" 8
" " , distal end, BB	" 9
Left " , " " , BB	" 11
Right scaphoid, A16	(No. 1)
" " , —	" 2
" " , BB	" 3
" " , D11	" 4
" " , BB	" 5
Left " , —	" 6
Right lunar, —	(No. 1)
" " , —	" 2
" " , —	" 3
Left " , —	" 4
Right cuneiform, —	(No. 3)
" " , —	" 6
" " , A16	" 7
Left " , BB	" 10
" " , —	" 11
" " , —	" 12
Pisiform, proximal end, —	
" , " " , —	
Right trapezoid, H11	(No. 1)
" " , —	" 2
" " , —	" 3
Left " , A16	" 5
" " , —	" 7
Right magnum, BB	(No. 1)
" " , B14	" 2
" " , —	" 3
" " , —	" 4
" " , —	" 6
" " , —	" 7
Left " , —	" 8
" " , —	" 9
" " , H11	" 10
Right unciform, A17	(No. 1)
" " , J7	" 3
" " , A16	" 4
" " , —	" 5
" " , —	" 8
Left " , A16	" 9
" " , E11	" 10
" " , —	" 11
" " , D10	" 12
Right metacarpal II, B13	(No. 1)
" " " , proximal part, BB	" 2
	" 3
" " " , proximal part, —	" 4
" " " , " " , —	" 5
Left " " , " " , —	" 7
" " " , " " , B14	" 8
" " " , " " , —	" 9
Right metacarpal III, —	(No. 1)
" " " , proximal part, B14	" 3
Left " " , A17	" 5
Right metacarpal IV, C14	(No. 2)
Left " " , A16, 17	" 4
" " " , C14	" 5
Left metacarpal V, BB	(No. 2)
" " " , C14	" 3
" " " , BB	" 4
" " " , mid-shaft missing, —	" 5

Left metacarpal II (No. 2) and left metacarpal III (No. 4) of one individual, A17.

Right metacarpal IV (No. 1) and the right metacarpal V (No. 1) of one individual, B14.

Rib, 65A

Partial sacrum and part of left os innominatum, A16.

Left femur, — (No. 1)
" " , — " 2
Right " , shaft only, juv., BB " 3
" " , distal epiphysis, — " 4
Left " , distal end, A16 " 5
" " , proximal part of shaft, BB " 6
Right patella, — (No. 1)
Left " , E10 " 3
Parts of five others, D11, D12, BB
Right tibia, A16 (No. 1)
" " , incomplete at end, — " 2
" " , BB " 3
Left " , proximal end of shaft, BB " 5
" " , lateral distal fragment, E10 " 6
Right fibula, 65C (No. 1)
Left " , 65C " 2
Right " , B15, 16 " 3
" " , proximal part, — " 4
Left " , distal end, — " 5
Right " , " " , — " 6
Left " , " " , — " 7
Most of right pes of one individual, including astragalus (No. 1), calcaneum (No. 1), navicular (No. 1), cuboid (No. 1), ectocuneiform (No. 1), mt. II (No. 1), mt. III (No. 1), mt. IV (No. 1), all phalanges except IV 3, and one sesamoid (No. 1); B15, 16.
Right astragalus, incomplete distally, — (No. 2)
" " , " " , A16, 17 " 3
Left astragalus, incomplete distally, A18 " 4
" " , " " , C12 " 5
Right calcaneum, BL (No. 2)
" " , A18 " 3
" " , A16, 17 " 4
Left " , BB " 6
" " , A16 " 7
" " , E10 " 8
" " , E12 " 9
" " , — " 10
Right navicular, — (No. 3)
Left " , C11 " 4
Right cuboid, D11 (No. 2)
" " , — " 3
" " , A16, 17 " 4
Right ectocuneiform, — (No. 2)
" " , A16 " 3
Left " , D11 " 4
" " , D11 " 5
Right mesocuneiform, D11 (No. 2)
Left " , — " 3
Right entocuneiform, D11 (No. 2)
Left " , — " 3
Right metatarsal II, BB (No. 2)
" " ", proximal part, — " 3
Left metatarsal IV, 65B (No. 2)
" " ", proximal part, D11 " 3
" " ", " " , A16, 17 " 4
Right " ", proximal end, D12 " 5
Median metapodial, distal end, E10 (No. 1)
" " , " " , B16 " 2
" " , " " , — " 3
" " , " " , — " 4
" " , " " , — " 5
" " , " " , A16, 17 " 7
" " , " " , D11 " 8
Lateral metapodial, distal end, — (No. 2)
" " , " " , — " 3
" " , " " , BB " 4
" " , " " , — " 5
" " , " " , — " 6
" " , " " , — " 7
" " , " " , — " 9
" " , " " , — " 10
" " , " " , — " 11
" " , " " , A16, 17 " 12
" " , " " , — " 13
" " , " " , — " 14
" " , " " , D11 " 15
" " , " " , D11 " 16
Phalanx 1, median digit, E10 (No. 1)
" , " " , — " 2
" , " " , — " 3
" , " " , — " 4
" , " " , BB " 6
" , " " , — " 8
" , " " , A16, 17 " 9
" , " " , — " 10
" , " " , A16, 17 " 11
" , " " , — " 15
Phalanx 2, median digit, E12 (No. 1)
" , " " , A16 " 3
" , " " , — " 4
" , " " , — " 5
" , " " , — " 6
" , " " , — " 7
" , " " , A16, 17 " 8
" , " " , — " 10
Phalanx 3, median digit
Phalanx 1, lateral digit, E10 (No. 1)
" , " " , A17 " 2
" , " " , — " 3
" , " " , A16 " 4
" , " " , BB " 6
" , " " , — " 7
" , " " , H10 " 8
" , " " , — " 9
" , " " , — " 11
" , " " , — " 12
" , " " , — " 13
" , " " , — " 14
" , " " , — " 15
" , " " , B14 " 17
" , " " , D11 " 18
" , " " , — " 19

Phalanx 2, lateral digit, — (No. 1)
" , " " , D11 " 2
" , " " , D11 " 3
" , " " , D12 " 4
" , " " , — " 5
" , " " , A16, 17 " 6
" , " " , A16, 17 " 7
" , " " , — " 8
" , " " , H11 " 10
" , " " , — " 11
" , " " , — " 12
" , " " , B14 " 14
" , " " , A16, 17 " 17
" , " " , — " 18

Phalanx 3, lateral digit; several incomplete specimens.

Proximal sesamoid, median digit, B15, 16 (No. 1)
" " , " " , A16 " 3
" " , " " , — " 4
" " , " " , — " 6
" " , " " , — " 7
" " , " " , — " 9
" " , " " , — " 10
" " , " " , — " 11
" " , " " , — " 12

Proximal sesamoid, lateral digit, D11 (No. 1)
" " , " " , — " 2
" " , " " , A16 " 3
" " , " " , — " 4
" " , " " , — " 5
" " , " " , D11 " 6
" " , " " , — " 7
" " , " " , — " 8
" " , " " , — " 9
" " , " " , — " 10
" " , " " , — " 12
" " , " " , — " 13
" " , " " , — " 14
" " , " " , — " 15
" " , " " , — " 16
" " , " " , — " 17
" " , " " , — " 18
" " , " " , — " 19
" " , " " , — " 20

At least eight individuals are represented. Numerous other bones were also collected from this quarry but are not listed since they do not add to knowledge of the species.

Field No. 57–64K, approximately 50 yards southeast of 70–64K and at same level. Found by B. Patterson. (This may be a continuation of the 70–64K quarry.)

Right radius, distal part (No. 12)
Left ulna, distal part (No. 10)
Right cuneiform (No. 1)
" " " 2
Left " " 9
Pisiform, proximal end
Left trapezoid (No. 4)
" " 6
Right magnum (No. 5)
Right unciform (No. 2)
" " " 6
" 7
Right metacarpal II, proximal part (No. 6)
Right metacarpal III, proximal part (No. 2)
Right metacarpal IV, proximal part (No. 3)
Right patella (No. 2)
Right tibia, distal end (No. 4)
Right navicular (No. 2)
Lateral metapodial, distal end (No. 1)
" " , " " (No. 8)
Phalanx 1, median digit (No. 13)
" , " " " 14
Phalanx 2, median digit (No. 2)
" , " " " 11
Phalanx 1, lateral digit (No. 5)
" , " " " 10
" , " " " 16
Phalanx 2, lateral digit (No. 9)
" , " " " 13
" , " " " 15
Proximal sesamoid, median digit (No. 2)
" " , " " " 5
" " , " " " 8
Proximal sesamoid, lateral digit (No. 11)

At least two individuals are represented.

Field No. 64–64K, approximately 20 yards east of and at same level as 70–64K. Found by C. T. Williams.

Incomplete mandible.

Field No. 68–64K, as for 64–64K. Found by W. D. Sill.

Right cuneiform (No. 4)
Right calcaneum (No. 5)
Right mesocuneiform (No. 1)
Median metapodial, distal end (No. 6)
Phalanx 1, median digit (No. 5)
" , " " 7
" , " " 12
Phalanx 2, median digit (No. 9)
Phalanx 2, lateral digit (No. 16)

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Osteology of the Malaysian Phallostethoid Fish *Ceratostethus bicornis*, with a Discussion of the Evolution of Remarkable Structural Novelties in its Jaws and External Genitalia

TYSON R. ROBERTS

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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OSTEOLOGY OF THE MALAYSIAN PHALLOSTETHOID FISH *CERATOSTETHUS BICORNIS*, WITH A DISCUSSION OF THE EVOLUTION OF REMARKABLE STRUCTURAL NOVELTIES IN ITS JAWS AND EXTERNAL GENITALIA[1]

TYSON R. ROBERTS[2]

ABSTRACT. The osteology of the phallostethoid *Ceratostethus bicornis* (Regan) is described and figured. Comparative observations on osteology of atherinoids, cyprinodontoids, and other phallostethoids are also given. Phallostethoids apparently originated from atherinids. The most closely related atherinids are Taeniomembrasinae. The osteological observations tend to support the idea that atherinoids and cyprinodontoids are related, as postulated by Rosen (1964) in proposing the order Atheriniformes. Atheriniforms exhibit a widespread tendency to develop teeth with two and three cusps, especially on the pharyngeal bones. The trend is pronounced in cyprinodontoids, exocoetoids, and scomberesocids, practically absent in atherinoids, and completely absent in phallostethoids and belonids.

The Phallostethoidea can be divided into two families, Phallostethidae and Neostethidae. Neostethidae comprises two subfamilies, Neostethinae and Gulaphallinae. These groups are distinguishable on the basis of morphological differences in the jaws and external genitalia. The highly protractile jaws of Neostethinae (as exemplified by *Ceratostethus* and *Neostethus*) are remarkable in having several pairs of bones without homologues in other fishes. These new bones, involved mainly in protrusion of the jaws, evolved in soft structures already present in the jaws of atherinids. The functional anatomy of the jaws of phallostethoids is briefly discussed. Phallostethidae and Gulaphallinae lack the neomorphic jaw bones found in Neostethinae. Two ctenactinia formed from pelvic fin spines or rays occur only in *Ceratostethus*. The so-called "second ctenactinium" of *Gulaphallus* is an externalized pelvic bone. Phallostethidae apparently arose from *Neostethus*. The toxactinium, the main externalized bony element in the priapium of Phallostethidae, is derived from the inner pulvinular bone, which is the anteriormost internal bony element in the priapium of Neostethidae. The inner pulvinular bone of *Neostethus* bears a small lateral projection, the pulvinular spine, which may be a rudimentary toxactinium. The structure of the papillary bone, intimately associated with the genital pore, is relatively simple in Gulaphallinae and Phallostethidae, but in Neostethinae it divides into numerous thin processes each bearing a hooklet at its tip. A comprehensive definition is given for the superfamily Phallostethoidea. All taxa used in this paper were proposed by previous authors.

Oviparous Atheriniformes with internal fertilization have external genitalia far more complicated than the gonopodium of any of the viviparous Atheriniformes. The explanation of this difference is sought in terms of selection pressures for and against the evolution of highly complicated external genitalia in forms with internal fertilization. Neotenic characters probably played an important role in the origin of phallostethoids from Atherinidae.

INTRODUCTION

Ichthyologists have marvelled at phallostethoids since they were first made known by C. T. Regan (1913; 1916). Males of these delicate little fishes from Southeast Asia can be distinguished in an instant by their strange subcephalic copulatory organ, or priapium, as Regan designated it. The 19 species now known have been divided

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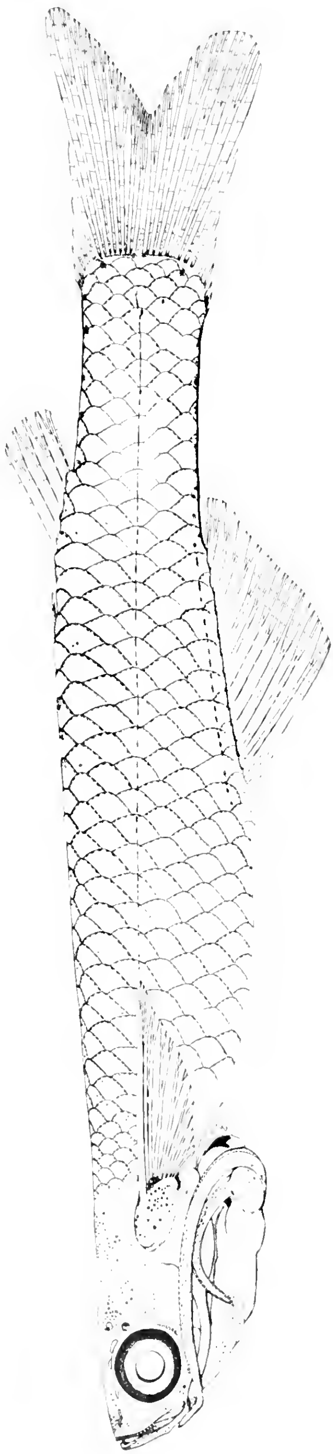


Figure 1. *Ceratostethus bicornis*, 25.3-mm sinistral male (MCZ 47305), from estuary of Chantaburi River, Chantaburi Province, Thailand.

into two families and ten genera, largely based on differences in the external armature of the priapium (see Herre, 1942). H. M. Smith (1927) made the surprising announcement that phallostethoids he observed in Thailand are oviparous. This discovery was confirmed in species from the Philippines by Villadolid and Manacop (1934) and Woltereck (1942a). Despite their outstanding interest, phallostethoids have remained virtually unknown to the general zoological public.

The present paper gives a relatively complete, illustrated account of the osteology of *Ceratostethus bicornis* (Regan) (Fig. 1), with special attention to the hitherto undescribed jaws and their functional anatomy. Previous osteological work on Phallostethoidea (with the exception of brief observations by Regan [1913; 1916], who lacked adequate skeletal preparations) has been almost totally restricted to the priapium (Bailey, 1936; Aurich, 1937; Woltereck, 1942a, b). The priapium is derived mainly from pelvic bones and fin rays, with contributions from the anteriormost ribs and pectoral girdle. The pelvic elements are so excessively modified that their homologies remain unresolved. This copulatory organ is perhaps even more specialized than the copulatory organs derived from the anal fin in the cyprinodontoids *Horaichthys* and *Tomeurus*. Interestingly enough, *Horaichthys* and *Tomeurus* are also oviparous, and they exhibit numerous morphological and ecological similarities to phallostethoids. The morphological similarities, however, do not extend to the jaws of *Ceratostethus:* although basically similar to the jaws of atherinoids, they are even more highly protractile and possess two major and two minor paired bones found so far in no other fishes except the closely related *Neostethus* (probably also present in *Solenophallus* and *Plectrostethus* and possibly *Phallostethus*, but absent in *Phenacostethus* and *Gulaphallus*). No observations have ever

been made on the feeding movements of *Ceratostethus* or any other phallostethoids; I have tried to determine the main features of their functional anatomy by manipulation of alizarin-stained specimens macerated in potassium hydroxide and cleared in 50 percent glycerine.

My initial objectives in studying the osteology of *Ceratostethus* were to provide information that might lead to a better understanding of 1) relationships of Phallostethoidea to other fish groups, and 2) relationships among phallostethoid genera. I chose *Ceratostethus* because, judging from priapial structure, it seemed to represent a relatively primitive phallostethoid, and I had an abundant supply of fresh material from Thailand. Regan (1913; 1916) regarded the phallostethoids as an aberrant subfamily of Cyprinodontidae, and noted that their osteology was "typically cyprinodontid." He did not indicate to which cyprinodontids they might be most closely related. Subsequent to the discovery by Herre (1925) that phallostethoids possess a spiny (albeit minute) first dorsal fin, most ichthyologists followed Myers (1928) in relating them to the Atherinidae. Myers intimated that Atherinidae and Cyprinodontidae might actually be fairly closely related, a suggestion generally viewed with disfavor (cf. Hubbs, 1944) until Rosen (1964) pointed out a large number of anatomical, morphological, and reproductive characters and trends common to atherinoids, cyprinodontoids, and allied forms (including Phallostethoidea) and united them in a new order, Atheriniformes. While placing the superfamily Phallostethoidea in the suborder Atherinoidei (*ibid.*: 261), he suggested that it might be more closely related to cyprinodontoids than to atherinoids after all (*ibid.*: 242). During the course of the present study numerous supplemental observations were made on cyprinodontoids and atherinoids. Phallostethoids apparently are more closely related to atherinoids than to cyprinodontoids. The most closely related forms appear to be *Stenatherina* and its Indo-Pacific allies (placed by Schultz, 1948, in the atherinid subfamily Taeniomembrasinae).

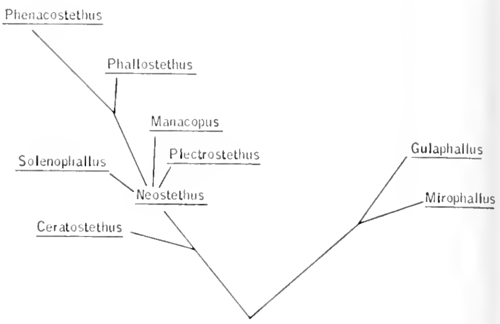
If one considers only zoogeographic distribution and priapial morphology (which has been worked out in considerable detail for almost all of the genera by Bailey [1936] and especially by Aurich [1937]), a relatively simple picture of phyletic relationships within Phallostethoidea emerges. There are two families: Phallostethidae and Neostethidae. Phallostethidae, presumably most highly modified from the primitive or ancestral type of phallostethoid, comprise two genera, *Phallostethus* and *Phenacostethus*, confined to the Malay Peninsula and adjacent parts of the mainland of Southeast Asia. Neostethidae comprise six to eight genera (Herre, 1942, probably went too far in splitting genera) belonging to two subfamilies, Neostethinae and Gulaphallinae. Gulaphallinae are restricted to the Philippines. Neostethinae, which include *Ceratostethus*, *Solenophallus*, *Plectrostethus*, and *Neostethus*, are more widely distributed. *Neostethus* and *Ceratostethus* occur in the Philippines, Borneo, and both sides of the Malay Peninsula.[1] The priapium of Neostethinae, in which the only externalized elements are derived from pelvic spines and rays, is evidently more primitive than are the priapia of Phallostethidae and Gulaphallinae. In phallostethid priapia the main externalized element is homologous with the neostethid outer pulvinular (Bailey, 1936; Roberts, 1971), which is the anteriormost internal element in the priapium of Neostethidae. *Neostethus*, alone among Neostethidae, has a single spur near the base of its ctenactinium, resembling the series of spurs on the ctenactinium of *Phallostethus* (the ctenactinium of *Phenacostethus* is absent or

[1] There are two records of indeterminable phallostethoids: from Sabang, northwestern Sumatra (Aurich, 1937: 282–284) and from Zamboanga (Banjagan, 1966: 46).

greatly reduced). In addition, the outer pulvinular bone of *Neostethus* has a small but distinct lateral projection, immediately anterior to the pulvinulus (absent in other neostethids), which might be an incipient or rudimentary toxactinium. Regan (1916: 6, fig. 3) referred to this projection as the pulvinular spine. It would be of great interest to compare the osteology of *Neostethus* and *Phallostethus*. Unfortunately, *Phallostethus* is represented in collections by only four type specimens in poor condition. The priapial characteristics of *Phenacostethus* have been treated in detail elsewhere (Roberts, 1971). Both *Gulaphallus* and *Ceratostethus* have been described as having two ctenactinia. The second ctenactinium of *Ceratostethus*, however, is evidently a modified pelvic spine or ray, whereas that of *Gulaphallus* is an externalized pelvic bone. In addition, in Gulaphallinae (*Gulaphallus* and *Mirophallus*) the anterior end of the ctenactinium fits into a fleshy sheath in the anterior end of the priapium, whereas in Neostethinae it remains uncovered (see Aurich, 1937: 266, figs. 1 and 2).

The discovery of neomorphic jaw bones in *Ceratostethus* and *Neostethus* adds a new dimension to the above sketch. Their presence in these genera and their absence in *Gulaphallus* indicate the distinctness of the subfamilies Neostethinae and Gulaphallinae and make direct derivation of Gulaphallinae from Neostethinae harder to conceive. Absence of the neomorphic elements is perhaps to be expected in the minute species of *Phenacostethus;* they may well be present in *Phallostethus*. Their absence in *Gulaphallus*, in which the jaws are distinctly less protractile than in *Neostethus*, *Ceratostethus*, and *Phenacostethus*, indicates that more diversity exists among Phallostethoidea than might otherwise have been thought.

The intergeneric relationships of Phallostethoidea, as currently understood, may be represented in a diagram as follows:



As previously indicated (Roberts, 1971), I am inclined to believe that the order Atheriniformes, as conceived by Rosen (1964), constitutes a natural assemblage. Thus far my researches have not uncovered any facts that cast serious doubt on this concept. Although Rosen (1964: 255) stated that the circumorbital series in Atheriniformes is represented only by lacrimal and dermosphenotic (lacrimal with separate ventral piece in a few cases), in some phallostethoids and atherinids there is a large, trough-shaped infraorbital bone immediately beneath the lacrimal, and in some atherinids (*Melanotaenia* and *Telmatherina*) there are two separate, troughlike or laminar infraorbitals below the lacrimal. Rosen (p. 288) found in melanotaeniids a small, spatulate element broadly and firmly joined to the ventral surface of the lacrimal, and noted that these two bones in melanotaeniids together resemble the single elongate lacrimal of *Xenopoecilus*. The second infraorbital bone (considering the lacrimal as the first infraorbital) in phallostethoids and atherinids observed by me is quite separate from the lacrimal. A first pharyngobranchial is present in *Ceratostethus*, *Melanotaenia*, and *Allanetta*, although Rosen (p. 237) stated that the first pharyngobranchial is lacking in Atheriniformes (*Melanotaenia* indicated as a possible exception). The Atheriniformes are diverse, and it is understandable that as additional representatives are studied more thoroughly, definitions will

have to be revised and expanded. It is undeniable that certain evolutionary trends, for instance those concerning reproduction, seem to be more readily understandable if the groups placed in Atheriniformes are indeed related. Thus some observations on the widespread occurrence of bi- and tricuspid teeth in Atheriniformes, which seem to confirm their relationship, are reported in this paper even though the dentition of phallostethoids is entirely conical. My own feeling, however, is that the concept of Atheriniformes should be verified by thorough osteological comparisons among the primitive or annectant representatives of the suborders assigned to it.

Villadolid and Manacop (1934) analyzed stomach contents throughout one year in wild-caught *Gulaphallus mirabilis*, and observed courtship, copulation, and egg-laying of this species in aquaria. These aspects of behavior have not been observed in any other phallostethoids. No new species of Neostethidae have been described since the genera and species were reviewed by Herre (1942). I reviewed the Phallostethidae, described a new species of *Phenacostethus* from the Indian Ocean coast of Thailand, and remarked upon the ecology of Phallostethidae and Neostethidae in Thailand. I also discussed the selective advantage of internal fertilization in Phallostethoidea as well as trends in the reproductive biology of atheriniforms that might be conducive to the evolution of internal fertilization (Roberts, 1971). The discussion section of the present paper deals with evolutionary topics such as the origin of the neomorphic jaw bones found in *Ceratostethus* and *Neostethus*, neotenic characters in phallostethoids, and the nature of selection pressures for and against the development of highly complicated external genitalia in atheriniforms.

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Miss Deborah White and Dr. Elizabeth Deichmann kindly translated the papers by Aurich and Woltereck. Much of the inspiration for the discussion section of this paper came from an essay on "The Emergence of Evolutionary Novelties," presented by Prof. Ernst Mayr at the Centennial Celebration of Darwin's *Origin of Species* in London (Mayr, 1960). Acknowledgment is gratefully made to Prof. George S. Myers. Prof. Myers acquainted me with phallostethoids when I was an undergraduate at Stanford University, and we have discussed them on numerous occasions.

OSTEOLOGY OF *CERATOSTETHUS* (Figures 2–12)

The following osteological account is based on 14 specimens (ten males and four females) 17.0–26.8 mm in standard length, part of a large series collected in a roadside ditch shaded by nipa palm about two miles from Tha Chalap on the road to Chantaburi City, Chantaburi Province, Thailand (MCZ 47304). The only osteological differences detected between males and females involve genitalia, and the anteriormost ribs and the cleithrum (modified in males to form a suspensorium for the priapium). The figures are based on four specimens, 24.8–26.8 mm. A few observations are included on the osteology of *Phenacostethus*, *Neostethus*, and *Gulaphallus*. Comments and comparative observations on cyprinodontoids and atherinoids

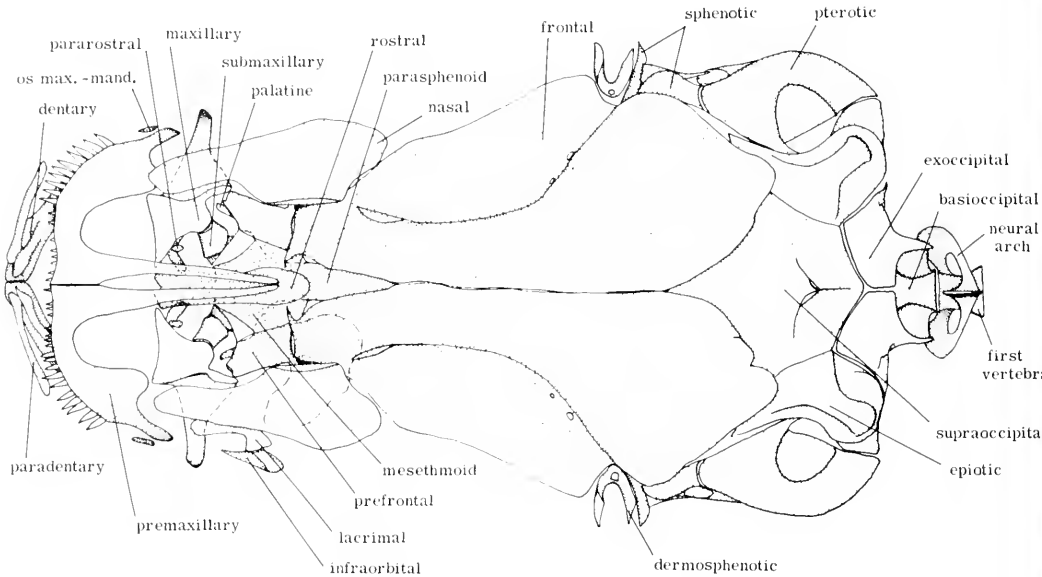


Figure 2. *Cerotostethus bicornis.* Dorsal view of skull and first vertebra; jaws slightly protruded.

are inserted in numerous places. I have examined alizarin preparations of a considerable variety of cyprinodonts (a number of them kindly provided by Neal Foster) and atherinoids (including alizarin preparations in the Department of Ichthyol ogy of the American Museum of Natura History). The osteology of atherinids in

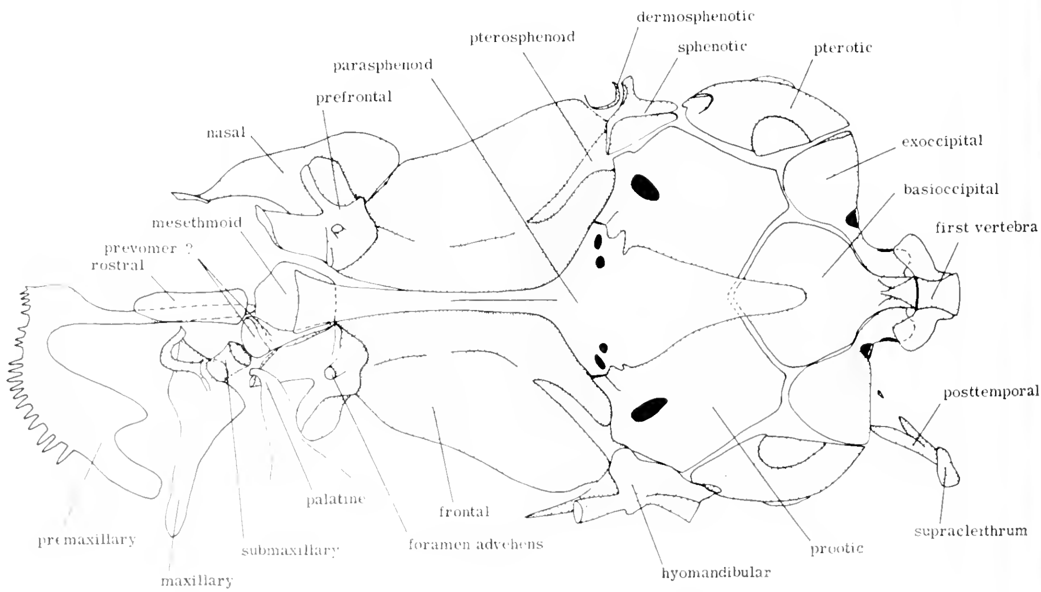


Figure 3. *Cerotostethus bicornis.* Ventrol view of cronium ond first vertebro; with portions of jows, suspensorium, anc shoulder girdle of right side.

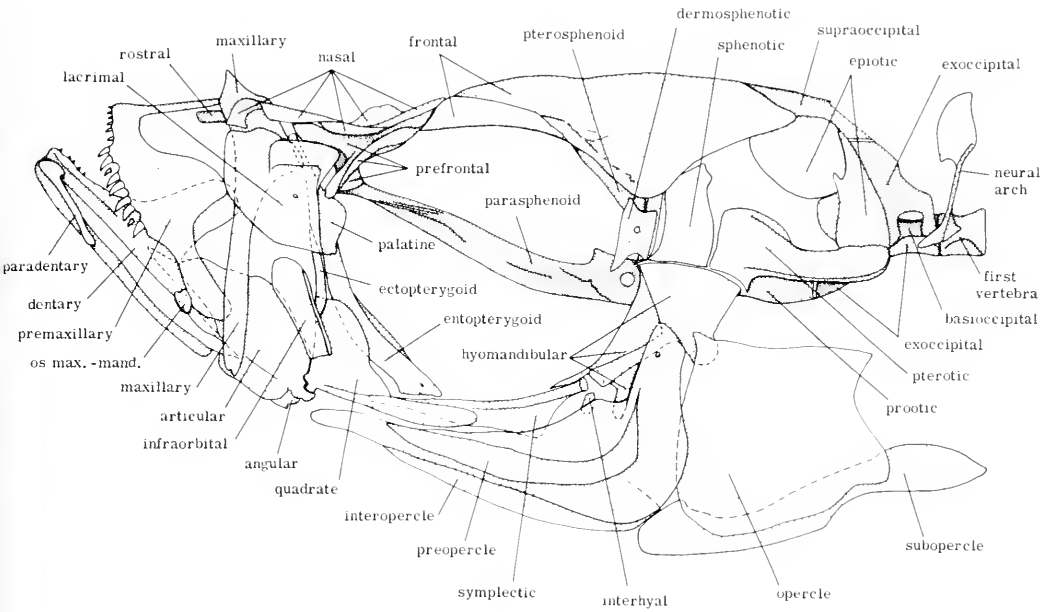


Figure 4. *Ceratostethus bicornis.* Lateral view of skull, first vertebra, and part of pectoral girdle.

the subfamily Taeniomembrasinae shows much in common with that of *Ceratostethus.* The parts of the skeleton are taken up in the following order: cranium, jaws, suspensorium, facial bones, hyoid and gill arches, pectoral girdle, median fins, vertebral column, and priapium.

Cranium (Figs. 2–4). Bones in cranium: prevomer, mesethmoid, prefrontals, frontals, parasphenoid, pterosphenoid, sphenotic, prootic, pterotic, epiotic, supraoccipital, exoccipitals, and basioccipital. Basisphenoid, parietals, and intercalar absent.

Anterior end of each side of prevomer enlarged and rounded to form a joint surface with submaxillary bone. In some specimens the prevomer is a single ossification. In others (including the ones in Figs. 2–4) it is ossified in two separate parts, one on each side of the mesethmoid. Mesethmoid a laminar bone of irregular hexagonal form. In some atherinids the mesethmoid is a thin lamina. (In cyprinodontoids mesethmoid either cartilaginous or a bilaminar ossification.)

Roof of skull convex, with a deep V-shaped trough between main body of frontal and supraorbital lamina; frontal bones depressed anteriorly where they meet prefrontals to form posterior floor of rostral fossa. In these features the roof of the skull resembles that of various atherinids; cyprinodontoids usually (always ?) have a uniformly flattened or only very slightly convex roof, without a trough between main body of frontal and supraorbital lamina. Skull roof smooth, without bony canals for cephalic laterosensory system; wings or crests absent excepting poorly developed (vestigial ?) supraoccipital crest. Supraoccipital spine undivided. Supraoccipital spine usually (invariably ?) undivided in atherinoids, bifid in cyprinodontoids (personal communication from D. E. Rosen). Dorsal border of foramen magnum formed exclusively by exoccipitals.

Jaws (Figs. 5–7). Although bearing strong morphological and functional resemblance to the highly protractile jaws of certain atherinids, the jaws of *Cerato-*

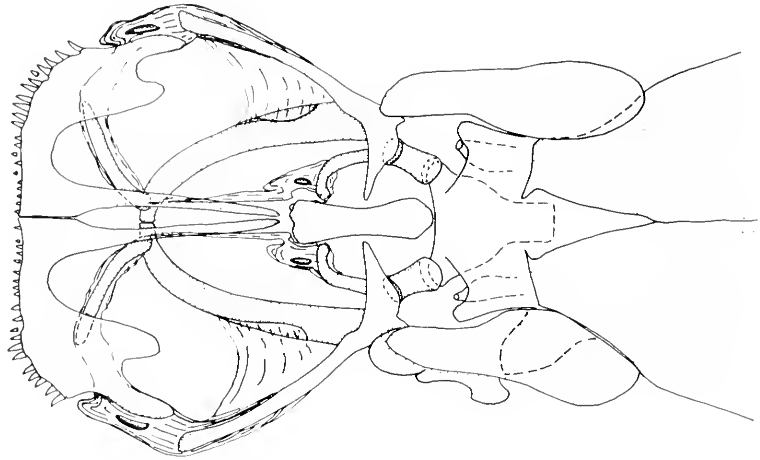


Figure 5. *Ceratostethus bicornis.* Dorsal view of anterior part of skull with jaws greatly protracted. Compare Fig. 6C.

stethus are perhaps even more specialized, for they include a number of hitherto unreported ossified elements, some of which are without known osseous homologues in atherinoids or cyprinodontoids or even analogues in other teleosts. These evidently neomorphic structures, apparently present only in phallostethoids, are functionally involved in the extreme protrusibility of the jaws (evidently including closure of the jaws in protruded position). The new bones, discussed below, are paired elements, named as follows (in order of occurrence anteroposteriorly): paradentary, maxillomandibular, pararostral, and submaxillary bones.

Bones in upper jaw: paired premaxillaries, maxillomandibularies, maxillaries, pararostrals, and submaxillaries; in lower jaw: dentaries, paradentaries, articulars, angulars, and coronomeckelians. Premaxillaries and dentaries with a single row of conical teeth; other jaw bones and palate toothless. Proximal third of premaxillary with eight to ten relatively small teeth, middle third with about ten enlarged teeth, distal third toothless. Dentaries with three to five very small (vestigial ?) teeth near symphysis; otherwise toothless. Ascending premaxillary processes slender, elongate (their length almost equal to a third of cranial length).

Posteriorly directed, broad-based, rounded processes ("articular processes") arising at midlength of premaxillaries; such processes (either rounded or pointed) characteristic of many atherinoids, are usually (invariably ?) absent in cyprinodontoids. Several atherinoids have slender elongate ascending processes as in *Ceratostethus;* ascending processes in cyprinodontoids usually (invariably ?) relatively short, broad-based, and wide. Maxillary with well-developed, strongly curved internal hooks. As in atherinoids (but not in cyprinodontoids) the maxillary has a laminar projection dorsal to the internal hook, part of which projects dorsally to the ascending premaxillary processes (when mouth is abducted). Lower (distal) limb of maxillary uniformly slender. A swelling (cranial condyle) at junction of internal hook with the main body of maxillary provides articular surface for submaxillary bone. Maxillary without ligamentous attachment to palatine. In atherinoids and in some (all ?) cyprinodontoids maxillary articulates directly to prevomer or to the ethmoid by a submaxillary meniscus. In atherinoids and cyprinodontoids there is usually (always ?) a direct ligamentou

connection between palatine and maxillary at or near cranial condyle. Head of maxillary bound in place, probably by ligamentous connections with nasal, lacrimal, and perhaps mesethmoid which, however, permit swinging and screwing movements. Lower (free) limb of maxillary uniformly slender. Internal hooks attached by dense connective tissue extending ventrally to rostral bone. Rostral connective tissue (ethmopremaxillary ligaments ?) with a pair of very small pararostral bones dorsolateral to anterior part of rostral bone. Near tip of lower limb of premaxillary, in the maxillomandibulary ligament lies the small, rounded, dorsoventrally compressed maxillomandibulary bone. The maxillomandibulary ligament connects the ends of the lower or free limbs of the premaxillary and maxillary to the dentary. The mouth is opened when movement originated by depressing the lower jaw is transferred by this ligament to the upper jaw. The attachment of the ligament to the dentary extends from middle of dentary to symphysis of lower jaws. Near symphysis main body of ligament very tough and round in cross section. In shape and extent of attachment the ligament resembles strongly that in certain atherinoids, particularly members of the subfamily Taeniomembrasinae (for definition and discussion of this taxon see Schultz, 1948). In other atherinids and in cyprinodontoids the attachment of the ligament does not extend much anterior to the middle of the dentary, and is spread out or sheetlike. The anterior part of the ligament in *Ceratostethus* differs strikingly from that in Taeniomembrasinae in that lying entirely within it is a very conspicuous and functionally significant ossification, the paradentary bone. Distal end of paradentary lies free in the ligament; its proximal end forms the ball of a ball and socket joint with the dentary at anteriormost point of attachment of ligament, i.e., near symphysis of lower jaw. Dentary with a high coronoid process, as in many atherinids; coronoid processes usually absent in cyprinodontoids.

In the following account I attempt to give an idea of functional (mechanical) relations of the jaw bones even though their movement was studied only in macerated specimens. I have assumed that in live specimens the mouth is opened mainly by depression of the lower jaw; that return of the jaws to normal "resting" position involves two distinct, consecutive stages, namely 1) closing of the mouth while it is still protracted, accomplished by retraction on the lower limb of the maxillary, drawing free ends and premaxillaries back (while position of lower jaw is unaffected), and 2) moving the entire assemblage back into the nearly vertical position it occupied before, probably accomplished by retraction on the coronoid process of the dentary and on the "articular process" of the premaxillary. From the work of Alexander (1966, 1967a, b) it seems likely that in many fishes with protractile jaws, the mouth is closed while the jaws are protracted. It is unclear whether the mouth can be closed when it is protracted in atherinoids, but it can be in some cyprinodontoids, as well as in cyprinoids, and acanthopterygians (Alexander, 1967a, b).

When mouth is in resting position, ascending premaxillary processes fit snugly into rostral concavity, their distal (free) ends lying between depressed anteriormost portion of frontal bones. When jaws are maximally protracted (as estimated by manipulation of KOH-macerated specimens) premaxillaries have moved forward about 125 percent of their length, or about 35 percent of the headlength.

Maxillaries of typically atherinoid form, excluded from gape and with well-developed internal hooks. With mouth completely closed, straight, slender ventral (distal) limb of maxillaries lies at an angle of about 10 degrees posterior to a vertical; with mouth fully protracted, ventral limb of maxillary at an angle of about 45 degrees anterior to a vertical (see Fig. 6A–C).

Screw movement is slight or nonexistent

Figure 6. *Ceratostethus bicornis.* Lateral view of jaws in varying stages of protrusion (for explanation see text).

until after more than half of the swinging movement is completed and the premaxillaries are considerably protracted. Up to this point movement of the premaxillaries is equal to that of the rostral; from this point on, however, the premaxillaries move relatively further forward than do the rostrals. Thus not only does the rostral slide forward relative to the cranium, but the premaxillary processes slide forward relative to the rostral; Alexander (1967b) found a similar movement present in *Atherina* but absent in the cyprinodontids *Aplocheilus* and *Fundulus.* Alizarin preparations of various cyprinodontids examined by me failed to exhibit this movement. The screw movement evidently also causes dilation of the lower limbs of the premaxillary, causing the lateral series of enlarged premaxillary teeth (which are directed sideways when the mouth is in resting position) to point straight ahead.

As stated by Alexander (1967b: 241) protrusion of the jaws must be accompanied by screw movement of the maxillary, so that the internal hooks and consequently rostral bone are moved anteriorly. In *Ceratostethus,* however, at least some protrusion occurs before the screw movement begins. Furthermore, it is possible to cause considerably more protrusion (about 25 percent more) after the rostral has ceased to move forward by simply continuing to depress the lower jaw. If this is done, the premaxillary tilts upwards posteriorly so that the mouth opening is slightly downwards instead of vertical. While it is doubtful that the jaws are normally protruded so far, this observation indicates that depression of the jaws can act unaccompanied by screw movements of the maxillary to bring the premaxillaries forward.

In cyprinodontoids the screw movement of the maxillary causes not only anterior movement of the internal hooks, but also lateral movement (Alexander, 1967b: 239 fig. 5). I have observed this in many cyprinodontoids. In *Fundulus* the rostral cartilage is Y-shaped, with the internal hooks attached firmly to the ends of the arms of the Y; as the internal hooks move laterally, the arms of the Y spread apart In addition, in many (but not all) cyprinodontoids, the internal hooks are so firmly bound to the ascending premaxillary that when the hooks move laterally, the ascending processes diverge posteriorly (see Alexander, 1967b, fig. 6e of *Fundulus*). In *Ceratostethus* there is either no lateral movement or very slight lateral movement of the internal hooks; the ascending pre

maxillary processes never diverge from each other.

Submaxillary process of maxillary articulated to prevomer by submaxillary bone (developed in place of the usual submaxillary meniscus). Submaxillary bone forms a meniscus with submaxillary process of maxillary and with anterior end of prevomer. When mouth is closed, submaxillary bone lies with its upper end at an angle of about 15 or 20 degrees anterior to a vertical; when mouth is protracted, rotation of maxillary depresses upper end of submaxillary, which finally lies at an angle of about 45 degrees from vertical with mouth fully protracted. The curved, ventrally directed internal hooks of the maxillaries are ligamentously attached to a median ossified element or rostral bone lying ventrally to ascending processes of premaxillaries. (This element evidently is represented by a rostral cartilage in atherinoids; it is similar in position, but not in movement, to the cyprinoid kinethmoid.) With mouth closed, anterior tip of rostral is horizontal with the anterior tips of the nasal bones and anterior margins of maxillaries; when mouth is fully protracted, it moves forward approximately 50 percent of its length. Above the rostral, in thickened connective tissue attaching it to ascending premaxillary processes and internal hooks of maxillary, lies a pair of small bones or pararostrals. These are evidently equivalent to accessory rostral cartilages of some atherinoids. Movement of pararostrals equal to movement of rostral.

Lower jaws similar in form to those in atherinoids: dentaries with very large coronary process, and with ventrally opened flange forming a trough for mandibular segment of cephalic laterosensory system. Maxillomandibulary ligament, linking tips of the ventral limb of maxillary and premaxillary to dentary, is similar to that in atherinoids (but not to that in cyprinodontoids) in that its connection to dentary extends anteriorly to ramus of lower jaws. In the maxillomandibulary ligaments of

Figure 7. *Ceratostethus bicornis*. Hypothetic closure of protracted jaws (for explanation see text).

Ceratostethus are two paired bones: the small maxillomandibulary bones, lying free in that part of the ligament connecting premaxillary and maxillary, and the elongate paradentaries, which are attached by a sort of ball and socket joint to the dentaries near ramus of lower jaw. Movement of the maxillomandibulary bones is dependent on movement of the premaxillary; their position with respect to lower limb of premaxillary remains unchanged. Maxillomandibulary bone forming conspicuous rounded prominence in angle of rictus of jaws when mouth fully opened (Fig. 6c). Paradentaries, with longitudinal axis parallel to that of dentary, lie snugly against dentaries in grooves; base of groove formed by dorsal surface of bony canal for mandibular segment of cephalic laterosensory system. With mouth about half open, paradentaries remain snugly against dentary; as mouth opens further, their distal (free) end swings sideways and upwards until, with mouth fully protracted, they are at right angles to dentary (Fig. 6c). When mouth closes in protracted position (closing accomplished in macerated specimens by pushing back on lower limb of maxillary), the paradentaries return to lie flush with side of dentaries, while only the lower limb of the premaxillary is retracted; the ascending premaxillary processes remaining as far or almost as far forward as they are when mouth is fully

opened (Fig. 7). Thus closure is accomplished almost entirely by movement of the upper jaw. The lower jaw remains depressed, the lower jaw bones, excepting the paradentary, undergoing little or no movement.

The paradentaries evidently are involved in increased protrusibility of the upper jaw. In specimens in which the maxillomandibulary ligaments have been cut immediately posterior to the distal end of the paradentaries, depression of the lower jaw still causes premaxillary protraction, but the premaxillaries do not project as far anteriorly and they project upwards (with leading margin considerably elevated) instead of straight forward. The paradentaries also help spread the gape sidewards as the mouth is opened.

Comments. Two objections that might be raised to this description of jaw function are 1) whether it is normal for the jaws to be so greatly protracted, and 2) whether closure actually occurs in the manner suggested. There are some fishes (including *Monocirrhus* among Nandidae [Liem, 1970], *Epibulus* among Labridae, several atherinoids) with protractile upper jaws and elongate ascending premaxillary processes in which the ascending premaxillary processes are advanced no more than a fraction (a half in *Epibulus;* about a third or less in *Monocirrhus* and the atherinoids) of their length when the jaws are fully protracted. In *Monocirrhus* and *Epibulus* (in which the lower jaws as well as the upper are protractile) the ascending premaxillary processes are exceedingly elongate—as long or longer than the total cranial length. The ascending premaxillary processes of *Ceratostethus* are relatively short compared to those of *Monocirrhus* and *Epibulus:* their length is about one-third of cranial length. Three facts indicate that the upper jaw is protracted as far or nearly as far forward as shown in Figure 5. First, protraction of the upper jaws this far is achieved by only moderate depression of the lower jaw. In various atherinoids and in the neostethid *Gulaphallus* in which the upper jaws do not protract very far, the mandible must be depressed further before the upper jaw moves forward at all than when the upper jaw is fully protracted in *Ceratostethus.* Second, the paradentaries do not rotate outward until the upper jaw is considerably protracted, and only slightly more forward movement of the upper jaw is involved for the paradentaries to rotate as far outward as in Figure 5. It seems to me highly likely that the paradentaries do in fact rotate this much. Third, when one depresses the lower jaw of a macerated specimen, the entire jaw assemblage moves readily and smoothly as far forward as in Figure 5. In particular, the motion of the maxillary is unencumbered. This contrasts with *Gulaphallus* and with various atherinoids in which movement of the maxillary is relatively restricted.

Whether closure of the jaws occurs in the manner indicated is much less sure. It seems likely that the jaws are closed in protracted position. Granted this happens, perhaps stages 1 and 2 envisioned in returning the jaws to resting position act in concert rather than consecutively. It may be that the mouth never closes with the upper jaw fully protracted (the position indicated in Fig. 7). It should be noted, however, that the jaws of macerated specimens are readily manipulated into this position, and that from this position they can be readily manipulated back to resting position, i.e., closed and completely retracted.

Liem (1970: 106), considering fishes with protractile jaws, stated that the salient features of feeding (and respiratory) movements are 1) opening and closing of the jaws, 2) protrusion of the jaws, 3) volume and pressure variations in the buccopharyngeal cavity, 4) abduction and adduction of the opercular apparatus, and 5) complex movements of the gill arches. He pointed out that these functions are mutually interdependent and should be considered in conjunction. Assessment of

the movements of the opercular apparatus and gill arches and their relationships in *Ceratostethus* has not been attempted, since "natural" movements of these parts are less readily achieved (or achieved with less confidence) by manipulation of macerated specimens. The main, or at least a major, advantage of protractile jaws may lie in increasing the buccal component of the buccopharyngeal pumping mechanism; one of the advantages in closing the mouth with the premaxillaries protracted probably lies in increasing the volume of water that can be sucked into the mouth without being forced back out as the mouth closes (see more detailed discussion in Alexander, 1967a: 59–62). It seems likely that these factors operate in *Ceratostethus*.

Suspensorium (Fig. 4). Bones in suspensorium: palatine, ectopterygoid, entopterygoid, quadrate, symplectic, and hyomandibular. Anterodorsal part of palatine slender, tubular, apparently connected by ligaments to prefrontal, but free of attachment to nasal, lacrimal, and maxillary. Movement of jaws fails to induce movement in palatine. Anterior margin of suspensorium (formed by palatine, ectopterygoid and quadrate) almost vertically inclined. Ventral portion of hyomandibular with processes contacting symplectic and preopercle. Symplectic with a ventrally directed laminar portion.

Facial bones (Figs. 2–4). Nasal well developed, almost as long as orbit, a dorsally projecting flange on its medial margin immediately lateral to depressed anteriormost portion of frontal, and a ventrally directed flange at its anterior tip that is intimately associated with anterodorsal corner of lacrimal bone. Circumorbital series comprised of lacrimal, a single infraorbital directly beneath it, and dermosphenotic. Lacrimal a large lamellar plate with a flange in its dorsoposterior corner forming a gutter for a segment of cephalic laterosensory canal. Ventral to lacrimal a single, concave infraorbital, forming a bony trough for a segment of cephalic

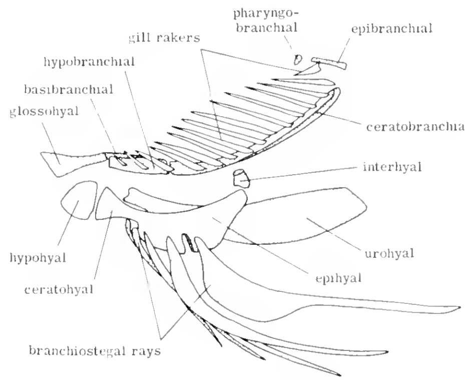


Figure 8. *Ceratostethus bicornis.* Lateral view of hyoid arch, urohyal, and first branchial arch. Hyoid and branchial arches slightly separated.

laterosensory canal. Dermosphenotic similarly troughlike, its attachment anterior to sphenotic (attachment of dermosphenotic posterior to sphenotic in *Horaichthys* and *Oryzias*). Preopercle with a ventrally open flange forming a trough for a segment of cephalic laterosensory canal. Opercle without spiny projections, its posterior margin concave as in some atherinids; in many (all ?) cyprinodontoids posterior margin of opercle broadly rounded. Posterior margin of gill cover formed by opercle, not by subopercle. Anterodorsal corner of opercle where it attaches to hyomandibular relatively unmodified, without a strongly reinforced socket to receive hyomandibular process. Interopercle and subopercle weakly ossified. Anterodorsal projection of subopercle weakly developed; posteriorly subopercle projects considerably beyond ventral margin of opercle.

Hyoid and gill arches (Figs. 8 and 9). Hyoid arch of typical atheriniform structure, with a single hypohyal; five branchiostegal rays on each side, first four branchiostegal rays attached to ceratohyal, last one to epihyal; dorsal half of joint between ceratohyal and epihyal strongly ossified; ceratohyal with a concave anteroventral margin. Gill arches with three median basibranchials, four pairs of hypo-

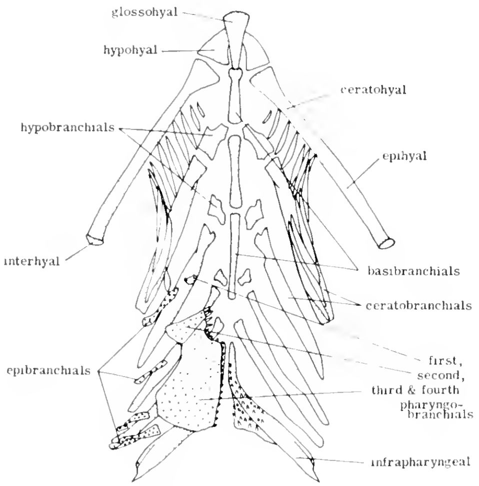


Figure 9. *Ceratostethus bicornis.* Dorsal view of hyoid arch (minus branchiostegal rays) and branchial arches. Uppermost branchial elements of right side removed.

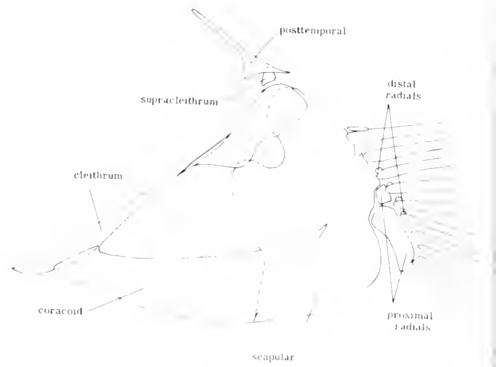
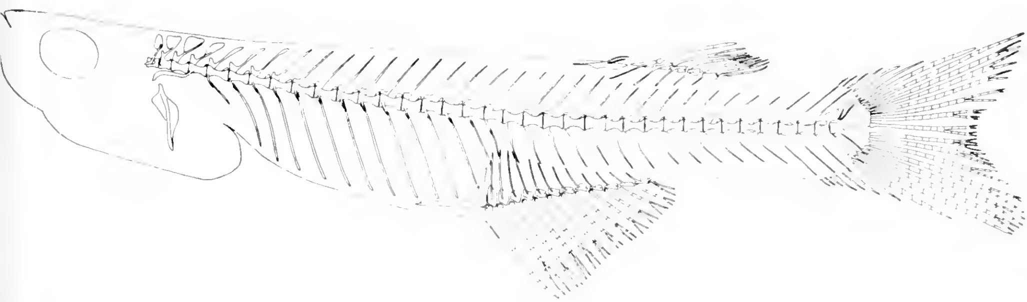


Figure 10. *Ceratostethus bicornis.* Lateral view of pectora girdle.

branchials, ceratobranchials, epibranchials, and pharyngobranchials, and a pair of infrapharyngeals. Third epibranchial T-shaped when viewed from side (figured only in dorsal view). Second, third, and fourth pharyngobranchials and anterior half of infrapharyngeals covered with moderately sized, irregularly arranged, conical teeth. Infrapharyngeals separate. Gill rakers only present on leading margin of first gill arch, 12 or 13 rakers on each side. First epibranchial bearing a single smaller raker, i.e., all rakers except this one are borne on lower half of gill arch. Anteriormost eight gill rakers on lower limb with distal ends directed laterally and posteriormost four or five rakers with distal ends directed increasingly medially, arrangement of these uppermost rakers thus simulating normal arrangement of rakers on upper limb of arch found in many fishes.

Pectoral fin (Fig. 10). Posttemporal forked; upper fork tightly bound to epiotic, lower fork short and not reaching base of cranium. Supracleithrum (as in other atheriniforms) a small scalelike element completely interposed between posttemporal and cleithrum. Cleithrum slender, only moderately expanded where it meet scapular to form scapular foramen, with out an expanded portion extending poste riorly to scapular. In mature males anterio limb of cleithrum elongated anteriorly, t almost double relative length of cleithrur in immatures and females, approximatin pulvinular bone of priapium. Cleithrum o one side elongated slightly more than tha of other side and ligamentously attached t pulvinular; at point of attachment slightl expanded to form a concave lamella fittin snugly over a convexity or bump in dorsa surface of pulvinular; anterior tip of op posite cleithrum ending in a fine poin Relative development of anterior prolon gation of cleithra variable. In some speci mens tip of cleithrum unattached t pulvinular falls far short of it, in other speci mens equal in length cleithrum attached t pulvinular. Laterality of cleithrum attache to pulvinular independent of laterality o priapium itself. Apart from this differenc in development of the cleithrum, the pec toral girdle is similar in males and female Anterior end of coracoid not prolonged i males. Posterior end of coracoid fused wit ventrally expanded portion of scapular, an not associated with radials of pectoral fir Postcleithra absent. Proximal radials two i number, lowermost considerably enlarged their proximal ends fitting snugly into concavity in posterior border of scapula



igure 11. *Ceratostethus bicornis.* Axial skeleton.

A series of about four small distal radials. An unpaired splint attached to proximal dorsal surface of uppermost pectoral ray. Pectoral rays 10 or 11.

Median fins (Fig. 11). First dorsal fin with two very short, slender, refractile spines; second spine even shorter and slenderer than first, attached to a pterygium consisting of a single element. Second dorsal with five segmented rays. First ray unbranched; last ray divided to its base, anterior division branched, posterior division simple. Second dorsal fin pterygials each consisting of a single element, with slender proximal and expanded distal portions. Anal fin with 14 or 15 elements, first element simple, short, and unsegmented, second long and segmented; third through penultimate elements branched, segmented rays; last element divided to base, both divisions simple. Form of anal fin pterygials as in second dorsal fin, except for enlarged anteriormost pterygial, which is prolonged anteriorly in ventral midline for a distance equal to eye diameter in front of anal fin origin. Caudal skeleton (Fig. 11) with two hypurals, both fused to hypural centrum. No epineural or urostyle. Two slender epurals. Penultimate vertebra with well-developed haemal spine but neural spine reduced to expanded basal portion only. Neural and haemal spines of vertebrae preceding penultimate vertebra equally slender and elongate. No accessory haemal spine or separate slender element interposed between haemal spines of antepenultimate and penultimate vertebrae (such an element present in *Dermogenys*, *Oryzias*, and *Xenopoecilus;* see Rosen, 1964, fig. 21). Caudal fin with 7 upper and 7 or 8 lower procurrent rays, and 7 upper and 7 lower principal rays, the outermost principal ray in each lobe unbranched. Posterior margins of hypurals straight and vertically aligned.

Vertebral column (Fig. 11). Vertebrae 35 or 36 excluding hypural; precaudal plus caudal either 18 + 17, 17 + 18 or 18 + 18. Distal ends of all except a few of the anteriormost and posteriormost ribs (which are associated with anteriormost pterygial elements of anal fin) meet opposite members in ventral midline of body. In females, anteriormost ribs are borne on third vertebra: first pair short and slender, without modified parapophyses; first three or four pairs of ribs gradually increasing in length. In males, first ribs borne on fourth vertebra. These ribs greatly expanded, their distal ends entering priapium just anterior to pulvinulus; parapophyses of fourth vertebra greatly enlarged, projecting anteriorly beneath vertebral column to a point below first and second vertebrae (Fig. 11). First three vertebrae without parapophyses. Ribs of fifth vertebra short and slender, their parapophyses unenlarged and posteriorly directed. Ribs of sixth vertebra of full length, reaching ventral midline of abdomen. Haemal arches not expanded (swim-

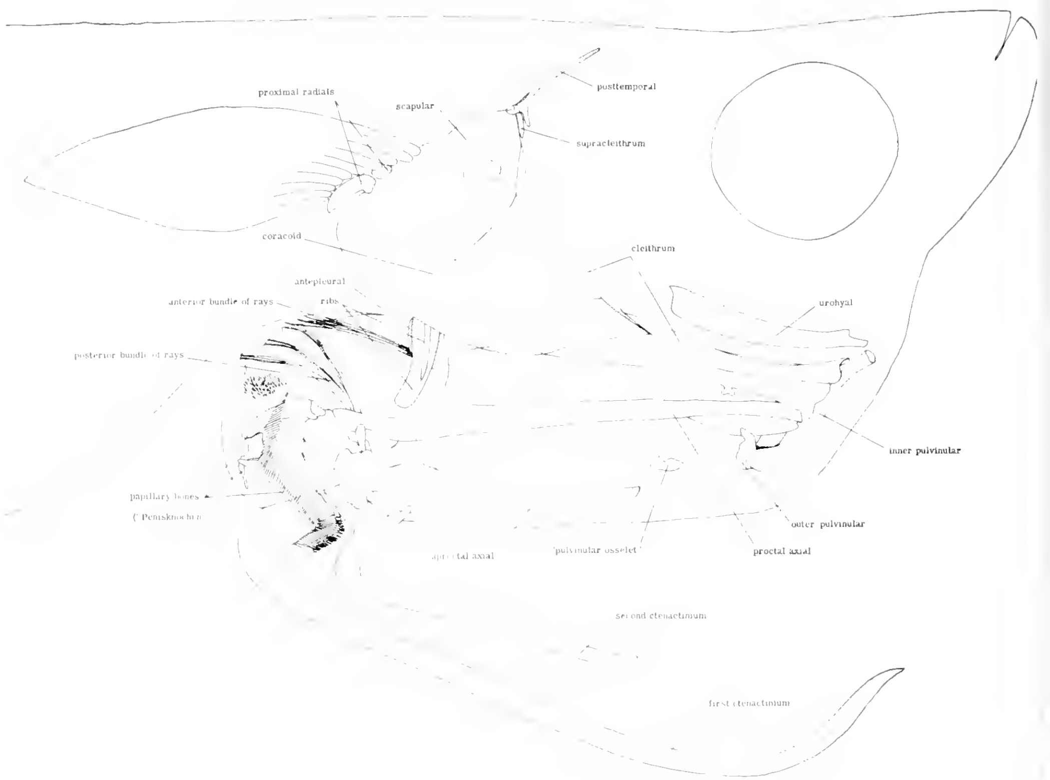


Figure 12. *Ceratostethus bicornis.* Lateral view of shoulder girdle, urohyal, and priapial skeleton of dextral male; ctenac tinia abducted.

bladder fitting snugly against posterior wall of abdominal cavity, without posterior projection into haemal arches). Intermuscular bones absent. First four vertebrae with distal ends of neural spines longitudinally expanded. Supraneurals absent.

Priapium (Fig. 12). The priapial skeleton of *Ceratostethus* is very similar to that of *Solenophallus* (Aurich, 1937) and *Neostethus.* The first and second ctenactinia of *Ceratostethus* evidently are homologous, respectively, with the ctenactinium and short, hooklike "Priapklaue" of *Solenophallus.* The anterior bundle of three segmented branched rays and posterior bundle of three segmented branched rays also are present. These rays lie in the wall of a sac that becomes filled with spermatophores. The branched ray tips protrude slightly from this sac, providing its posterior mar gin with a "fringe" or "comb."

As in *Solenophallus*, the main element in the axial skeleton of the priapium ar the two pelvic bones. The proctal pelvi bone (i.e., the one opposite the ctenactina is considerably enlarged and acts as th suspensorium of the entire priapium. It i suspended anteriorly by the outer pulvin ular and inner pulvinular ("Pulvinulus träger" of Aurich), which are in tur suspended by the attachment of the pulvin ulus to the cleithrum and perhaps also th urohyal. The inner pulvinular is absent i *Gulaphallus* and *Mirophallus* (cf. Bailey 1936; Aurich, 1937). Posteriorly it is sus pended from the vertebral column by it ligamentous attachment to the antepleura cartilage and anteriormost modified rib

(see Aurich, 1937, fig. 3 of *Solenophallus*). The proximal ends of rays in posterior ray bundle firmly articulated to side of posteriormost part of proctal pelvic bone. Aproctal pelvic bone movably articulated to proctal pelvic bone by a series of complicated bones, the morphology of which is difficult to make out in intact priapia (see also Aurich, 1937). Two ctenactinia movably articulated to aproctal pelvic bone. Lying between anterior end of aproctal pelvic bone and accessory pulvinular is a small bone, the pulvinular osselet, evidently homologous with the pulvinular cartilage in *Solenophallus*. At the posterior end of the priapium, in the axis of the ctenactinia, is a series of excessively modified bones surrounding or partly surrounding the genital pore. These elements represent the "dorsal," "middle," and "ventral penisbones" of Aurich. In *Ceratostethus* and *Neostethus* the "ventral penisbone" gives rise to a large number of straight, thin bony projections, constituting a sort of flap over the genital pore. Many, if not all, of these projections are doubled back at the tip, and end as a hooklet. In *Neostethus* the projections, about 80 in number, are parallel to one another. In *Ceratostethus* the projections are much more numerous, some are considerably enlarged, and at each end of the genital pore a large number of the projections are oriented away from the main body of projections. The "ventral penisbone" of *Solenophallus ctenophorus* is similarly modified. It evidently is homologous with the greatly enlarged "ventraler Penisknochen" of *Gulaphallus* (called papillary by Bailey, 1936), with the slender "ventraler Penisknochen" of *Mirophallus*, and perhaps with the enlarged papillary bone in the base of the penis in *Phenacostethus*. In *Gulaphallus*, *Mirophallus*, and *Phenacostethus*, however, the parallel projections and hooklets are absent.

Plectrostethus Myers (1935) is said to be closely related to *Neostethus*, "from which it differs trenchantly in the presence of the spine-bearing process of the priapium and in the wing-like margin of the ctenactinium." The ctenactinium has a broad membranous margin along the lower side of its proximal half. At the base of the ctenactinium is a flat fleshy process armed on its upper and posterior border with a row of nine or ten short sharp recurved spines and on its anterior border by two longer spines directed forward (Myers, 1935: 5–6). The flat fleshy process is presumably homologous with the "ventral Penisbone" (= papillary bone ?) of *Ceratostethus* and *Neostethus*. The only known specimens of *Plectrostethus* are 12 type specimens of *P. palawanensis* Myers (U. S. National Museum nos. 93421–93423).

CHARACTERIZATION OF THE SUPERFAMILY PHALLOSTETHOIDEA

This characterization of Phallostethoidea is based on a survey of the literature and my own observations on *Phenacostethus* (both species), *Ceratostethus bicornis*, *Neostethus siamensis* (probably equals *N. lankesteri*) and *Gulaphallus mirabilis*. My observations have been relatively complete only for *Ceratostethus*. Many, if not most, of the characters cited below can be found scattered in the literature; virtually all of these characters have been verified by me, and erroneous statements in the literature rectified (e.g., concerning the pectoral girdle and first pleural ribs). The characters are presented in the following order: 1. general body features, size, habitat; 2. reproduction; 3. sensory organs; 4. squamation; 5. fins; 6. skull and visceral arches; 7. dentition; 8. pectoral girdle; 9. vertebral column (including ribs and intramuscular bones).

1. Largely translucent, bilaterally compressed and moderately elongate, tiny or very small, atheriniform fishes, adults from 14 (*Phenacostethus smithi*) to 37 mm (*Gulaphallus eximus*) in standard length (females usually slightly larger than males). Inhabiting fresh to brackish, usu-

ally turbid, coastal streams of mainland and insular Southeast Asia, usually within range of the tides.

2. Oviparous; gonad single; fertilization internal, males with a clasping and intromittant organ, the priapium, derived mainly from the pelvic fins; pelvics evanescent, vestigial or absent in females. In males anus opens on side of priapium opposite genital pore, in females anal and genital openings close together on throat. Eggs demersal, chorionated, with adhesive filament (not verified in Phallostethidae); sperm transferred in large masses held together by a mucoid substance (spermozeugma), at least in Neostethidae. Newly hatched young are miniatures of adults, probably immediately capable of active feeding and swimming.

3. Eyes large, laterally directed, free from orbital rim. Nostrils, if present, minute (a single opening which may be a nostril lies on the side of the snout near the upper jaw in *Neostethus* but is apparently absent in *Ceratostethus;* olfactory lamellae are not evident beneath the skin of the snout). A large pore midway between tip of snout and anterior margin of eye in Neostethidae is evidently a pore opening into supraorbital canal of cephalic laterosensory system. Cephalic laterosensory system well developed, supraorbital, preorbital, postorbital, preopercular, and mandibular canals with large pores in Neostethidae. In Phallostethidae laterosensory organs on top of head housed in a membranous dome, evidently without pores (see Roberts, 1971). Lateral line canal absent on body. Otoliths absent (dissolved by formalin ?). Contact organs absent.

4. Scales cycloid; body except "neck" completely scaled; scales in lateral series 31–58. Head scaleless or sparsely scaled, scales on head confined to posterior border of skull roof and preopercle.

5. Pectoral fin set high on sides of body, its shape slightly falcate, with ten or eleven rays. First dorsal fin usually present (absent in *Mirophallus, Solenophallus thessa* and perhaps absent in *Phallostethus*), consisting of one or two tiny, weak (nonerectile ?) spines movably articulated to an elongate pterygium. The second spine, when present, usually even thinner and shorter than the first. First dorsal completely separated from second dorsal, but much closer to it than in atherinids, its origin posterior to a vertical through anal fin origin. Second dorsal with one or two simple, unbranched, segmented rays (no spines), and three to nine branched rays. Origin of second dorsal well behind anal fin origin, or even posterior to anal fin. Anal fin with a short flexible spine, followed by an unbranched, segmented ray and ten to 28 branched rays. Initial pterygiophore of anal fin an enlarged backwards L-shaped bone (Fig. 11). A translucent median, abdominal, membranous keel invariably present. Caudal fin forked; in at least some species the upper lobe is slightly longer than the lower lobe and is pointed, while the lower lobe is rounded (Fig. 1; Roberts, 1971, figs. 2 and 3 of *Phenacostethus*); principal caudal rays from $5+7$ or $6+7$ to $7+8$ or $8+8$.

6. Upper jaw usually highly protractile. Mesethmoid a single, irregularly hexagonal lamina; intercalar absent; parietals absent; infraorbital series represented by lacrimal, second infraorbital and dermosphenotic; dermopalatine absent. Lower arm of maxilla separated from mandible by expanded lower arm of premaxilla; maxillomandibulary ligament round in cross section where it attaches to dentary, the attachment near symphysis of lower jaws. Hind border of opercle concave; opercle and preopercle without spines or serrations; interoperculum not extending posterior to vertical from preopercle or overlapping subopercle. Distal half of ceratohyal abruptly expanded, a dorsal bridge of bone joining it to epihyal; branchiostegal rays four or five; gill rakers present only on leading edge of first gill arch, other arches rakerless.

7. Teeth strictly conical, confined to

premaxillary, dentary, second through ourth pharyngobranchials, and infra-pharyngeals. Teeth on premaxillary and lentary in a single row (*Ceratostethus, Veostethus, Phenacostethus*) or in two to our rows (*Gulaphallus*). Dentition of ower jaw well developed in *Gulaphallus*, poorly developed (vestigial ?) in *Cerato-tethus* and *Neostethus*.

8. Supracleithrum a small bone sand-viched between posttemporal and dorsal ip of cleithrum; cleithrum without wing-ike dorsal expansion; scapula and coracoid used together; only two proximal pectoral adials or actinosts, the lowermost en-arged; cleithra extended anteriorly in nales, one or both of them attached to pulvinular bone of priapium.

9. Vertebrae 34 to 38. In Neostethidae he numbers of precaudal and caudal verte-brae are about equal. In Phallostethidae caudal vertebrae more numerous than precaudal: *Phenacostethus* with 14 to 16 precaudal and 19 or 20 caudal, *Phallo-stethus* with about 10 precaudal and 28 caudal vertebrae. First pair of ribs borne on third vertebra in females and on fourth vertebra in males of *Ceratostethus, Neo-stethus*, and *Phenacostethus*. In *Gulaphallus mirabilis* (MCZ 33904) a 23.1-mm immature nale and a 22.0-mm specimen that appears o be an immature female both have the first ribs on the fourth vertebra. First pair of ribs in males greatly enlarged and at-tached to axial support of priapium; par-apophyses of aproctal priapial rib enlarged and directed anteriorly so that its distal end, to which the rib is attached, lies be-neath second vertebra. Intramuscular bones absent.

Comments. The Phallostethoidea con-stitute a distinctive and well-defined taxon. Almost all of their characters are in reason-able agreement with Rosen's concept of the Atheriniformes, with the (probably minor) exception of number of pectoral radials and relationship of the scapula and coracoid. Within the Atheriniformes it appears to be most closely allied to the atherinoids, and within atherinoids, to the subfamily Taeniomembrasinae. The sug-gestion by Rosen (1964: 242) that phallo-stethoids might be more closely related to cyprinodontoids than to atherinoids was based solely on the erroneous idea that the first pair of pleural ribs in phallostethoids originated on the second vertebra. In phallostethoids, as in many (all ?) ather-inoids, the first pair of ribs is borne on either the third or the fourth vertebra, whereas in cyprinodonts the first pair of ribs is usually (invariably ?) borne on the second vertebra. It is noteworthy that the lowest vertebral count in atherinoids is 31, only three less than the lowest count in phallostethoids, whereas a number of cyprinodontoids have as few as 26. Cyprin-odontoids usually (invariably ?) have intramuscular bones, while at least some (but not all) atherinids agree with phallo-stethoids in lacking them. Various other points in which phallostethoids agree with atherinoids more than with cyprinodontoids have been pointed out in my osteological description of *Ceratostethus*. Among the most important of these are the basically similar morphology of the jaws and at-tachment of the maxillomandibulary liga-ment to the dentary.

While phallostethoids are the only Atheriniformes known to me in which the first pair of ribs is ligamentously attached to the pelvic girdle, a ligamentous connec-tion between the pelvic girdle and the distal ends of a pair of ribs evidently is a primitive atheriniform character. Which pair of ribs is attached depends mainly on the position of the pelvic girdle. Thus the ribs attached to the pelvic girdle are the third pair in *Melanotaenia*, the fourth in *Telmatherina*, the fifth in *Fluviphylax*, the sixth in *Menidia*, etc.

According to Bailey (1936: 464), in *Gulaphallus mirabilis* the distal ends of the first pair of ribs are "embedded in a heavy triangular mass of fibrocartilage, the ante-pleural cartilage, which is attached by fibers to the posterior crest of the axial

bone." In *Phenacostethus* (*ibid.*: 472) the tips of the priapial ribs are embedded in the antepleural cartilage, "which is ossified throughout most of its length and forms a distinct rod-like antepleural bone." An ossified antepleural is present in *Ceratostethus* and *Neostethus*. In atherinoids and cyprinodontoids a "secondary postcleithrum" is intimately associated with the distal end of each of the first pair of ribs. There is no trace of this element in female phallostethoids, and none in males either, unless it corresponds with the antepleural. The antepleural cartilage or bone of phallostethoids is perhaps neomorphic. The inner pulvinular bone of *Ceratostethus* and *Neostethus*, which apparently gave rise to the phallostethid toxactinium, probably is neomorphic. It apparently has no homologue in atherinoids. For a discussion of the homologies of the priapial elements see Woltereck (1942b: 343–347).

The haemal spines of the anteriormost caudal vertebrae are expanded to permit extension of the swimbladder posterior to the abdominal cavity in various exocoetoids (only in the family Exocoetidae ?), cyprinodontoids, and atherinoids. In phallostethoids the swimbladder extends to, but not beyond, the posterior wall of the abdominal cavity (as in taeniomembrasines), and the haemal spines are unexpanded.

The single gonad of Phallostethoidea (observed in *Phallostethus* and *Neostethus* by Regan [1916], in *Phenacostethus* and *Gulaphallus* by TeWinkel [1939]) is probably a primitive character widespread in atheriniforms. The gonads are usually (invariably ?) single in cyprinodonts, including *Oryzias, Rivulus, Fundulus*, and others.

The teeth of phallostethoids, both on the jaws and in the pharynx, are evidently invariably simple conical teeth, as one would expect in fishes of their tiny size. Hence, they fail to exhibit one of the most persistent trends of the atheriniforms, namely possession of tricuspid teeth.

Widespread occurrence of tricuspid teeth in atheriniforms. While most atheriniforms have conical jaw teeth, bi- and tricuspid teeth occur in the jaws of diverse representatives; this is especially true in cyprinodontoids but is not confined to them. Miller (1956: 8–9) hypothesized that tricuspid teeth evolved independently at least three times in New World cyprinodontids, and suggested that the Old World cyprinodontid genera with tricuspid teeth also originated independently. Tricuspid jaw teeth occur in some genera of Poeciliidae; the outer row of jaw teeth of Jenynsiidae has tricuspid teeth. Bicuspid jaw teeth characterize the atherinid genus *Atherinops*, and tricuspid jaw teeth occur in some genera of Exocoetidae and Hemiramphidae. The significance of these facts has not been fully appreciated, because the remarkably widespread occurrence of bi- and tricuspid pharyngeal teeth in atheriniforms has passed virtually unnoticed. Garman (1895, pls. I–V) showed that practically all cyprinodontoid groups exhibit a considerable variety of tooth forms in the jaws and pharyngeals; in a number of instances the pharyngeal teeth exhibit considerably more variation in form than the jaw teeth. *Anableps*, for example, has conical jaw teeth, but the pharyngeal teeth exhibit a wide variety of forms including tricuspid. Many cyprinodonts with conical teeth in the jaws nevertheless have some pharyngeal teeth of bi- or tricuspid form. *Pantanodon podoxys*, with no trace of jaw teeth, has tricuspid teeth on the pharyngeals, even in specimens only 17 mm in standard length (Whitehead, 1962, fig. 8). As one might expect, however, the smallest cyprinodontids and poeciliids usually have simple conical teeth in both jaws and pharynx. This does not seriously detract from the generalization that most, if not all, groups of cyprinodontoids have the tendency to develop bi- and tricuspid teeth and that this is seldom completely suppressed. This generalization can be extended to include most groups of atheriniforms. Thus tricuspid teeth occur on the pharyngeals in exocoetids and hemiram-

hids (some of which also have tricuspid aw teeth) and in scomberesocoids (jaw eeth usually or invariably conical; verified n *Scomberesox saurus*). Belonidae ex- mined by me have conical pharyngeal eeth; the conical pharyngeal teeth of everal belonids are figured by Collette 1966, figs. 2 and 3). The pharyngeal teeth f adrianichthyoids are conical (verified in *Xenopoecilus poptae* and *X. sarasinorum*). Throughout the atheriniforms, the smallest orms are likely to have simple conical eeth (e.g., phallostethoids, *Oryzias*); again, his does not seriously detract from the generalization that atheriniforms have a emarkable predisposition to develop bi- nd tricuspid teeth.

DISCUSSION

The protractile jaws of phallostethoids. The diversity of jaw mechanisms in teleosts s becoming ever more apparent. Probably nore neomorphic joints and bones have risen in the jaws than in any other of the najor teleostean functional anatomical units (as defined by Liem, 1967). A great nany of these structural innovations are ssociated with mobility of the upper jaw. t has been estimated that the jaws are protractile in about half of the living eleosts. While the majority of forms with protractile upper jaws are acanthopteryg- ans, paracanthopterygians, or cyprinoids, protractile upper jaws also occur in Atheriniformes, in the gonorhynchoid *Phractolaemus*, and the characoid *Bivibranchia*. The functional mechanism of protractility is completely different in acanthopterygians, cyprinoids, *Phracto- laemus* and *Bivibranchia* (for acanthopte- rygians, see Alexander, 1967a; Liem, 1970; Osse, 1969; Schaeffer and Rosen, 1961; for cyprinoids, Matthes, 1963; Alexander, 1966; or *Phractolaemus* and *Bivibranchia*, Géry, 1963). The functional mechanisms in atheriniforms are relatively similar to those n acanthopterygians. Although both per- nit protraction of the upper jaws, the attachments and movements of the acanthopterygian rostral and cyprinoid rostral or kinethmoid are radically dif- ferent. As fishes with protractile jaws are studied more closely, additional evo- lutionary novelties are bound to be dis- covered. For example, in *Epibulus insidiator* (family Labridae) the lower jaw is just as protractile as the upper jaw. As might be expected, this extraordinary adaptation involved major changes in the suspensorium. The outstanding jaw mech- anisms of many teleosts remain equally uninvestigated. Some of the most peculiar jaws occur in tropical inshore fishes for which no observations on feeding have been recorded, and suggestions as to how the jaws are used would necessarily be fairly speculative.

To my knowledge, no other fishes have bony structures comparable to the paraden- taries and submaxillaries of Neostethidae. The rostral bone of neostethids is probably homologous to the rostral cartilage of acanthopterygians, and cartilaginous ele- ments similar to or homologous with the pararostrals occur in atherinoids (accessory rostral cartilages). Analogous rostral car- tilages or bones and accessory rostral cartilages occur in cyprinoids. Bones anal- ogous to the submaxillaries occur in Cobitidae. The maxillomandibulary bones are small bones, and similar elements in other fishes, if they occur, are likely to have been overlooked. A small bone similar to the maxillomandibulary bone, but lying dorsal to the lower limb of the maxillary instead of ventral to it, occurs in the characoid *Chilodus*. Such "supramaxil- lary" bones probably have evolved inde- pendently in numerous lines. The presence of such an element in *Chilodus* cannot be construed as a primitive character.

The paradentaries and submaxillaries are large elements, obviously of considerable functional significance. They are evidently involved in increasing the extent to which the jaws can be protracted. The paraden- taries probably are also important in keep-

ing the mouth wide open when it is fully protracted and perhaps in permitting the upper jaw to close down over the lower jaw while the lower jaw remains fully depressed. The paradentaries are joined by a ball and socket joint to the dentaries near the symphysis of the lower jaw, and are capable of rotating outward 90 degrees and upward 45 degrees from their resting position in a trough on the side of the dentary. The submaxillaries are tubular bones with a meniscus at either end: the anterior meniscus with the maxillary bone, the posterior meniscus with the prevomer.

Although novel as bony elements, the paradentaries and submaxillaries arise in structures that are characteristic of atheriniforms, and particularly of atherinoids, the group to which they seem most closely related. Furthermore, the paradentary bones and submaxillary bones can be seen as the ultimate consequences of clearly defined evolutionary trends exhibited in atherinoids. Thus the anteriormost part of the maxillomandibulary ligament in some atherinoids (notably in the Taeniomembrasinae) has the peculiarities of the anterior part of the maxillomandibulary ligament in phallostethoids except that no paradentary bone develops in it. That is, in these atherinids the attachment of the ligament to the dentary is extremely far forward, near the symphysis; the body of this portion of the ligament is tough and round in cross section, and when the mouth is closed it lies in a trough on the side of the dentary identical with the trough in which the paradentary bone lies in neostethids. Concerning the submaxillary bone, it evidently serves much the same function as the submaxillary meniscus in atherinids. Alexander (1967b: 234) found the submaxillary meniscus much thicker in *Atherina* than in *Melanotaenia;* in *Atherina* "the submaxillary meniscus can swing anteriorly and somewhat medially about its articulation with the cranium, carrying the cranial condyle of the maxilla anteriorly and ventrally" (*ibid.*: 236). Movement of the submaxillary bone and maxillary in neo stethids is similar but of greater magnitude

The condition of the prevomer should b noted. In almost all fishes this dermal bon is a single, median element. In *Cerato stethus,* however, it sometimes ossifies i two pieces that remain separate, each wit its anterior end greatly expanded where i is joined by a meniscus to the submaxillar bone. While dermal bones usually maintai their integrity, it is not impossible for them to give rise to separately ossifying element Frazzetta (1970) described and discusse the subdivision of the maxillary bone t form two maxillary bones united by a intramaxillary joint in bolyerine snakes.

Neotenic characters of phallostethoid In teleosts it is extremely unusual for th anus and urogenital openings to be place anterior to the pelvic fins. In most teleost in which these openings lie at the throa the pelvics are either absent or are eve farther forward than the openings. In thi respect phallostethoids are exceptional. I males and in females in which the pelvic are vestigial or evanescent, anal an urogenital openings are morphologicall anterior to pelvic fins. In adult atherin oids the position of the openings i variable, but they always lie posterior t the pelvic origin. It may be immediatel in front of the anal fin, distinctly in front o it, or even between the pelvic fins. Wolte reck (1942a: 256) made the importan discovery that the openings lie anterior t the pelvic fins in larval *Atherina.* This sug gests that the condition in phallostethoid may be neotenic.

It may well be that the anterior positio of the pelvic fins, and perhaps even thei attachment to the shoulder girdle, ar neotenic, at least in part. In atherinoid thought to be primitive, *Rheocles* an *Bedotia,* the pelvics are relatively far for ward. The ancestors of atherinoids ma have had the acanthopterygian characte istic of thoracic pelvic fins connected wit the shoulder girdle.

The subcephalic position of the priapiur

cannot, however, be ascribed entirely to neoteny. No atherinoids or atheriniforms of any kind have the pelvics anywhere near as far forward as they are in phallostethoids. The anteriad prolongation of the cleithrum and of the parapophyses of the fourth vertebra in male phallostethoids indicates that the priapium has "migrated forward" (in an evolutionary sense). The selective advantage of an anteriorly located, i.e., subcephalic, priapium may lie in greater visual coordination during mating.

The phallostethoid "neck" may also be considered a neotenic character, for it appears to result in large part from absorption of the yolk. In larval phallostethoids the compact yolk sac lies immediately posterior to the head; it occupies considerable space where the neck eventually forms.

Almost certainly neotenic is the phallostethoid abdominal keel, derived from the median embryonic fin fold. In larval phallostethoids the fin fold extends continuously from its origin at a point on the dorsum about midway between snout and caudal base (where the first dorsal fin arises), around the caudal lobe and then on the ventrum uninterruptedly until it ends at the posterior margin of the yolk sac (see Villadolid and Manacop, 1934, pl. 2, fig. 2, pl. 3, figs. 1 and 2 of larval *Gulaphallus mirabilis*). In adult phallostethoids the abdominal keel consists of actinotrichia (the fibrous rays characteristic of embryonic fins).

The abdominal keel presumably plays the most important of the hydrodynamic roles formerly played by the pelvic fins. If, as may have been, acquisition of the abdominal keel permitted phallostethoids to utilize the pelvic fins for an entirely new function, it was a key step in their evolution.

Evolution of complicated external genitalia. Internal fertilization is a regular feature in the reproductive biology of many groups of atheriniforms (excepting Phallostethoidea, these groups belong to the Cyprinodontoidea). In three groups—Poeciliidae, Goodeidae, and Jenynsiidae-Anablepidae—it has led to viviparity. Gonopodial morphology in these viviparous forms ranges from relatively simple in Goodeidae and in the poeciliid tribe Poeciliini to remarkably complex in the poeciliid tribe Cnesterodontini (see Rosen and Bailey, 1963, for figures of the poeciliid gonopodia). It is a striking fact that in the three groups that evolved internal fertilization and are oviparous—Tomeuridae, Horaichthyidae, and Phallostethoidea—the primary copulatory organ is far more complex than in any of the viviparous forms.[1] The gonopodium of *Tomeurus* can be compared directly with that in Poeciliidae, since *Tomeurus* is evidently related to the poeciliids and its gonopodium is derived mainly from the same rays in the anal fin as the poeciliid gonopodium. Perhaps the most complicated gonopodium in any poeciliid is that of the cnesterodontin *Phallotorynus*, which bears an enlarged scooplike element at its tip (*ibid.*, fig. 31a, b). The gonopodium of *Tomeurus* is much more complex: its tip bears a pair of greatly enlarged antlerlike processes, a far more complicated scooplike arrangement, and the distal end of the fifth anal ray, which is modified in a manner recalling the even more greatly modified papillary bone of neostethids (*ibid.*, figs. 7, 13–16). The gonopodium of *Horaichthys* (Kulkarni, 1940), which evolved independently of the gonopodium of Poeciliidae and Tomeuridae, is as complicated as that of *Tomeurus*. The neostethid priapium is morphologically as complex as or even more complex than the gonopodia of *Tomeurus* or *Horaichthys*, and far more complicated than the gonopodium of any of the viviparous forms. The question may now be raised, why are these structures in oviparous forms more complex? Conversely, why have viviparous

[1] The situation is admittedly complicated by the development in viviparous forms of modified pelvic or pectoral fin structures that function as accessory copulatory structures, but this does not seriously alter the main theme under consideration.

forms failed to evolve gonopodia as complicated as those in oviparous forms? The puzzle increases when we recall that the gonopodium of *Horaichthys* is not an intromittant organ but serves only to convey spermatophores with dartlike attachments that are implanted externally near the female's vent.

It would seem that perfection of the organs of fertilization would be just as important to viviparous forms as to oviparous ones; and yet nature has favored the more complicated structures in oviparous forms, and selected against their development in the viviparous forms.

The explanation of this seemingly contradictory state of affairs perhaps lies in two considerations: first, effects on mating behavior of differences in the habitats occupied by oviparous and viviparous atheriniforms, and second, deleterious effects of excessively complicated external genitalia. Evidence concerning these factors was gathered during my fieldwork on phallostethoids in Thailand.

In Thailand neostethids and phallostethids occur only a short distance inland, in waters strongly influenced by tides. Usually the current is strong and the water muddy. They are swift swimmers, generally stay in midwater and can maintain themselves in the current. During flood waters they are likely to be widely dispersed. Thus several hours of collecting at Khlong Langu in Satul Province during high tides combined with heavy rain yielded only a half-dozen immature *Neostethus,* all taken singly. Whenever either *Ceratostethus* or *Neostethus* were found during low water, they were usually aggregated and sometimes exceedingly numerous (as in the estuary of Chantaburi River, where *Neostethus* and *Ceratostethus* were found together in large numbers). When the tide is out, *Ceratostethus* are likely to be confined to well-defined creeks and channels; when the tide is in, they are probably dispersed over a wide area of partially submerged mangroves and nipa palm. *Horaichthys* and *Tomeurus* apparently occur in comparable habitats, *Horaichthys* along the Bombay-Kerala coast of India, *Tomeurus* along the northeastern coast of South America, including the mouth of the Amazon. The selective advantage of internal fertilization in these fishes may lie in permitting temporal separation of mating and egg-laying, corresponding, respectively, with periods of low water and high water (Roberts 1971). It seems likely that mating in such habitats is difficult, because of current and low visibility. The waters in which these fishes live are probably especially turbid during the rainy season, when mating probably reaches its peak. In this connection it is noteworthy that copulation in *Gulaphallus mirabilis* is prolonged, the male clasping the female for one to two minutes (Villadolid and Manacop, 1934: 200).

In contrast to phallostethoids, poeciliids tend to occur in habitats in which mating can occur much of the time and under relatively favorable conditions. Poeciliid gonopodial thrusts are relatively short in duration, some almost instantaneous; they may be repeated several times without sperm transfer and often strike wide of the mark, perhaps even more in some forms with less specialized gonopodia. Yet such males are undoubtedly quite efficient at fertilizing females; the number of females in populations of poeciliids is generally greatly in excess of that of males.

In all my collections of neostethids, males outnumbered females. In places where they were particularly abundant, it was sometimes possible to catch 25 or 50 at once, and in these instances the ratio of males to females was sometimes about equal. From some places where individuals were relatively scarce or collecting was particularly difficult, collections of half-a-dozen or dozen specimens of *Ceratostethus* are entirely males. During fieldwork it appeared that 1) males of neostethids are at least as abundant, if not more abundant, than females, and 2) males are more readily caught because the priapium prevents them

from swimming away as quickly as females. This suggests that males are more susceptible to predation than females. It seems probable that the exceptionally large gonopodia of *Horaichthys* and *Tomeurus* would encumber their swimming.

Another disadvantage of highly complicated genitalia may lie in an increased proportion of developmental anomalies. Developmental anomalies in the priapium of phallostethoids are probably relatively frequent. Woltereck (1942a) mentioned, but did not describe, developmental anomalies in the priapia of neostethids from the Philippines. I find a number of anomalies in my material, including a *Neostethus* with a peculiarly bowed ctenactinium (which could not be properly swung into resting position beneath the head) and additional externalized elements or "supernumerary ctenactinia" and a *Ceratostethus* in which the priapium is equally developed (but not fully formed) on both sides.

Finally, the development of a large external genitalium requires a considerable diversion of energy and materials, and such "expenditures" will always be selected against unless they confer a selective advantage. The highly complicated copulatory organs presumably ensure successful sperm transfer with each copulatory episode. In fishes in which copulatory episodes are rare this will have great selective advantage.

Provided environmental conditions are such that internal fertilization has a selective advantage, there is little to prevent its development in fishes. There are numerous records of internal fertilization occurring in fishes, such as trout, which normally have external fertilization; sperm simply enter the oviduct and fertilize eggs within the female. Such occurrences do not lead to the evolution of internal fertilization, but are selected against, when the life history strategy of the fishes involved overwhelmingly favors external fertilization. Oviparous atheriniform fishes, on the other hand, which tend to have relatively small numbers of eggs that are expelled in small batches or even singly, and in which embryonic development or hatching can be deferred, may be preadapted to the evolution of internal fertilization (Roberts, 1971). If internal fertilization is favored, then every modification of pelvic or anal fins (no matter how slight) that increases the probability of sperm entering the oviduct will confer a selective advantage. Thus the stage is set for intensification of function (Mayr, 1960), which eventually can lead to structures as complicated as the priapium and papillary bone of *Ceratostethus bicornis*.

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Revision of the North American Ciidae (Coleoptera)

JOHN F. LAWRENCE

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REVISION OF THE NORTH AMERICAN CIIDAE (COLEOPTERA)

JOHN F. LAWRENCE

CONTENTS

ABSTRACT

A taxonomic revision is made of the 12 genera and 84 species of Ciidae known to occur or likely to occur within the confines of the continental United States and Canada. Discussions of the family limits, phylogenetic relationships, zoogeographic origins, and host relationships are also included. Keys are given to subfamilies, genera, and species. For each North American species, an informal diagnosis, distributional summary, and summary of host records are presented. The following generic synonymies are proposed: *Cis* Mellié (= *Eridaulus* Thomson syn., = *Macrocis* Reitter syn.); *Hadraule* Thomson (= *Maphoca* Casey syn.); *Malacocis* Gorham (= *Brachycis* Casey syn.). Type species are designated for the following genera: *Eridaulus* Thomson (*Anobium nitidum* Fabricius); *Macrocis* Reitter (*M. taurus* Reitter). The following new species are described: *Cis* **acritus**, *Cis* **cayensis**, *Cis* **cornelli**, *Cis* **crinitus**, *Cis* **discolor**, *Cis* **festivulus**, *Cis* **megastictus**, *Cis* **niedhauki**, *Cis* **robiniophilus**, *Cis* **rotundulus**, *Cis* **stereophilus**, *Ennearthron* **aurisquamosum**, *Hadraule* **explanata**, *Ceracis* **magister**, *Ceracis* **pecki**, and *Rhopalodontus* **americanus**. In addition, 31 new species synonymies are proposed and 12 new combinations are made.

INTRODUCTION

The Ciidae is a relatively small, cosmopolitan family of small to minute beetles,

which feed in both larval and adult stages on the mycelia and fruiting bodies of wood-rotting fungi, such as Polyporaceae. At present, the family includes about 40 genera and 550 species, but the generic concepts badly need revision and at least 400 more species remain to be described. The following paper consists of a short, general section on the taxonomy of the group and a more detailed account of the 12 genera and 84 species known to occur or likely to occur within the confines of the continental United States and Canada. Throughout the text, this area will be referred to as North America, even though Mexico has been excluded. The keys and discussions presented should permit the identification of the vast majority of ciid species encountered north of the Mexican border, but there are probably a number of undescribed forms yet to be found in southern Florida, along the Gulf Coast of Texas, and in the mountains of the Southwest.

Although the scope of this work is limited geographically, the concepts presented are derived from an examination of large numbers of specimens from various parts of the world. The generic treatment is relatively conservative, and with the exception of a few obvious synonymies (*Cis-Macrocis, Hadraule-Maphoca, Malacocis-Brachycis*), no drastic changes have been made in the classification currently used in the United States. The recognition of Casey's *Orthocis* and *Plesiocis* and Dury's *Dolichocis* and *Strigocis*, however, is contrary to the concepts of European workers. In Lohse's work (1967), *Orthocis* and *Strigocis* would be included in *Cis* and *Sulcacis*, respectively, while species of *Dolichocis* and *Plesiocis* would be placed in *Ennearthron*.

Brief sections are included on the geographic distribution and host preferences of North American Ciidae, but these topics (particularly the latter) will be covered in more detail in a future publication (Lawrence, in preparation).

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METHODS AND TERMINOLOGY

Taxonomic Characters

Color is of limited diagnostic value in the family, except when large samples are available for comparison, and it has been used to distinguish only a few forms with obvious elytral markings. When color is given in descriptions, simple English words are used and Latin terms are avoided. Vestiture has been used extensively in this work, especially at the species level, since it usually is subject to little geographic variation (except in *Cis creberrimus*, p. 452). The vestiture is said to be single if it consists of one type of element (bristles, hairs) and dual if there are two distinct types (bristles and hairs, erect and inclined

bristles, Figs. 29 and 30). The individual elements vary from short, fine hairs or short, stout scales to long, recurved hairs or long, erect bristles. In certain genera (*Ceracis, Octotemnus*) and species groups (*Cis tricornis* group, *Cis pacificus* group) the vestiture remains fairly constant, whereas in others (*Cis nitidus* group, *Cis taurus* group) it is subject to considerable variation, even among closely related species. The lengths of individual elements are usually compared to the basal width of the scutellum.

Head characters are used primarily for males (see below). The vertex is defined as the entire area between the eyes from the frontoclypeal ridge to the concealed occiput. In most ciids, the area in the vicinity of the frontoclypeal or epistomal suture forms a ridge extending from eye to eye (Fig. 3); this is called the frontoclypeal ridge and is composed of both frons and clypeus.

The antennae may be 8-, 9-, or 10-segmented, with a 3-segmented club, although the first club segment is reduced in *Hadraule blaisdelli.* The number of segments is diagnostic at various levels and their relative lengths may be of value at the specific level (ratio of III to IV is used in descriptions). The antennal club segments in the Ciidae are characterized by having at least four large, sensilla-bearing processes, here called *sensillifers* (Figs. 1 and 2). These structures, which have been referred to as "sensory pores" (Casey, 1898; Scott, 1926) or "ampoules à trichoïdes" (Lesne, 1935), appear to be homologous to the hygroreceptors of *Tribolium* (Roth and Willis, 1951a, 1951b) and the "organe sensoriel" of *Typhlophloeus* and *Hypophloeus* (=*Corticeus*) (Jeannel and Paulian, 1945). I have seen similar structures in various tenebrionids (Gnathidiini, Diaperini, Ulomini, Strongyliini), *Myrmechixenus* (Colydiidae), and *Cryptophilus* (Languriidae). These organs may be useful at the generic level but are here restricted to the family diagnosis. Maxillary palps may also prove useful, but they are not used extensively in the present treatment.

The pronotum varies considerably in relative size and shape, with rounded to subparallel sides. The lateral margins may be very narrow to broad and explanate (Figs. 24 and 22), and in some species there is a raised lip at the edge (Figs. 18 and 43). The edge itself may be smooth (Fig. 43) or crenulate (Fig. 44). The anterior angles (where the dorsal and lateral edges meet) may be rounded (Fig. 15) or produced and angulate (Figs. 14, 18, and 22). The pronotal disc varies in surface sculpture and punctation. The surface is smooth and shiny or granulate and dull. and the punctures vary in both diameter and density. The average diameter is compared to either an eye facet or the base of the scutellum, and as an index of density, the spaces between punctures are expressed in terms of puncture diameters.

The elytra also vary in relative size and shape, with parallel to rounded sides and blunt to subacute apices. In *Orthocis* and *Strigocis,* the elytral suture bears an inflexed apical margin (Fig. 38). Elytral punctation may be single (punctures relatively uniform in size and depth and all bearing bristles or hairs) or dual (punctures falling into two classes differing in size and depth, with only one bearing bristles or hairs). The punctures vary in distribution from confused to seriate, and also in coarseness and density.

The prosternum has been used extensively, especially at the generic level. The subfamilies Ciinae and Orophiinae are distinguished mainly by the structure of the prosternum and procoxae (*see* generic key p. 436), and the genera of Ciinae are usually distinguished on the basis of prosternal characters. The portion of the prosternum in front of the coxae may be long (Fig. 28) to very short and striplike (Figs. 25 and 27), while the intercoxal process may be broad (Fig. 26) or laminate (Fig. 24), and parallel-sided (Fig. 23) or tapering behind (Fig. 27). In the Orophiinae, the inter

coxal process is very short (Fig. 25) and the procoxae extend well behind and below it (Fig. 16). The anterior part of the prosternum also varies in cross section, being concave or biconcave (Figs. 9–10) and on a different level than the intercoxal process (Fig. 15), or flat to carinate (Figs. 11–13) and on the same level (Fig. 14). The procoxae are almost always open behind (Figs. 22–25; 27–28), but in members of the *Cis vitulus* group the postcoxal bridges meet the intercoxal process to form a posterior closure (Fig. 26). In all Ciidae, the procoxae are open internally.

Tibiae have been used extensively in this group, and the apex of the protibia is particularly diagnostic. The outer apical angle may be narrowly rounded (Fig. 45), dentate (Fig. 50), or expanded and bearing several stout spines (Fig. 58). In addition, the outer edge of the protibia may be spinose (Fig. 60) or serrate (Fig. 54). Spines may also occur at the inner apex (Fig. 54), but they are found in most species and are of little diagnostic value (these are excluded from most illustrations). Although the protibial apex is a useful character at generic and specific levels, it must be treated with caution in certain groups because of sexual differences.

The metasternum varies in shape and convexity, while the metasternal suture varies in length and may be absent (Fig. 33). The hindwing is relatively simple with reduced anal region and a subcubital fleck; it exhibits little variation within the family, but some exotic ciids may be brachypterous or apterous. Genitalic characters have been studied in the male only and consist of the eighth abdominal sternite and the aedeagus. The latter consists of a small basal piece, a ventral tegmen, and a dorsal median lobe (Figs. 85 and 86). The latter two structures and sternite VIII have been included in most descriptions, but these genitalic characters are rarely used in the keys. The terminology is taken from Sharp and Muir (1912), but Lindroth (1957) should be consulted for alternative names.

Secondary Sexual Characters

In the great majority of ciid species, males have a pubescent, glandular structure in the middle of the first visible abdominal sternite (III), which is here called a *pubescent fovea* or *abdominal fovea*, but which has been variously referred to as a "tubercule velu" (Abeille de Perrin, 1874b), "setigerous fovea" (Casey, 1898), "behaartes Grübchen" (Reitter, 1902a), "setiferous pit" (Miyatake, 1954), "median depression" (Kevan, 1967), "setigerous pore" (Lawrence, 1967b), and "Auszeichnung" (Lohse, 1967). The structure may be simple (Fig. 32), margined, or raised and tuberclelike, and in the Orophiinae it may be covered by a triangular flap (Fig. 31). Similar abdominal structures are found in males of many different beetles, including Erotylidae (Delkeskamp, 1959), *Sphindocis, Dermestes,* and *Blaps* (Meixner, 1934). In the Ciidae, it varies in size and shape and is useful mainly at the species level. The greatest diameter or length of the fovea may be compared to the "body" of sternite III or that portion of the sternite behind the intercoxal process. Among the North American ciids, the following species lack the fovea in the male: *Cis congestus, C. horridulus, C. hystriculus, C. huachucae, C. subtilis,* and *C. vitulus.*

Pubescent foveae may also occur on the vertex of the head of the male. This is the case in *Dolichocis manitoba,* the *Cis pacificus* group, and the "*Ennearthron*" *filum* group. Median and/or lateral tubercles occur on the male vertex in some species, such as *Cis niedhauki* (Fig. 5) and certain *Xylographus* and *Octotemnus.*

The frontoclypeal area is relatively simple in most Orophiinae, but in the Ciinae the development of a frontoclypeal ridge provides a good taxonomic character for species and species groups. This ridge may bear two teeth or tubercles (Fig. 40), two triangular plates (Fig. 39), two long horns (Fig. 42), a median horn (Fig. 6), four teeth (Fig. 4), or a raised, trisinuate

plate (Fig. 3). The anterior edge of the pronotum is also modified in some species, forming a median process (Fig. 41) or two horns (Fig. 7). There are many different types of frontoclypeal and pronotal ornaments, and a particular type is often characteristic of a species group. The major difficulty in using these characters is that they tend to vary allometrically, so that those of larger males may differ greatly from those of smaller ones and the latter may be similar to those of females or small males of related species.

Modifications of the mandibles occur only in the Orophiinae and in no North American species. *Xylographus* males may have a tooth on the left mandible, while in certain Old World *Octotemnus* both mandibles are enlarged.

Measurements and Ratios

Pronotal length (PL) is measured along the midline and in males includes horns or laminae. Pronotal width (PW) is the greatest width. Elytral length (EL) is taken just to one side of the midline and from the base of the scutellum to the elytral apex. Elytral width (EW) is the greatest combined width of both elytra. Greatest depth (GD) is taken through the elytra and metasternum. The total length (TL) is the sum of PL and EL and does not include the head; it is given in millimeters. For one sample of each species described, the range, mean, and standard error of the mean are given for TL and for the following ratios: TL/EW, PL/PW, EL/EW, EL/PL, and GD/EW. In the descriptions, these ratios are given for the holotype and allotype and in the keys they are used only when there is little or no overlap between alternatives. They have proven very useful in distinguishing between species and even higher groups of Ciidae, because of the large amount of variation in general body form occurring in the family. Other ratios included in descriptions are: antennal segment III/IV; prosternal intercoxal process width/procoxal cavity width; length/width of metasternum; length of metasternal suture/median length of metasternum (including its anterior process); and, length of abdominal fovea/median length of sternite III (body only, excluding its anterior process).

Observations and Drawings

Observations were made of dried, fluid-preserved, and slide-mounted material with the aid of a Leitz stereoscopic microscope (12.5× and 18× oculars, 1×, 2×, 4×, 8×, and 12× objectives) and a Bausch and Lomb compound microscope (10× oculars, 100× and 440× objectives). Measurements were made with an ocular linear micrometer, and drawings were made with the aid of ocular grids in the eyepieces of both microscopes. Initial drawings were transferred from graph paper to white board and inked with a series of rapidograph pens. In most of the drawings, no attempt has been made to show relief, and stippling or solid shading has been used to set off specific areas (coxal cowling, abdominal fovea, eyes) or to indicate pigmentation (aedeagus, sternite VIII). Dotted lines have been used to indicate a sharp bend in a surface (raised frontoclypeal ridge, lateral pronotal margin) or a hidden outline (protibial apex, sensillifers, overlapping abdominal sternites).

Synonymies and Descriptions

Synonymies have been reduced to include only author, date, and page, but complete references are cited in the terminal bibliography. The species synonymies are relatively complete, but generic synonymies include only major works. Complete descriptions are given for new species only; for previously described forms and for all genera a short diagnosis is included in the discussion. The species description is usually based on the holotype and is followed by a brief indication of differences in the

allotype. The male genitalia figured are not those of the holotype but have been dissected from one of the male paratypes. The protibiae illustrated have also been removed from paratypes.

Variation

Each species description is followed by a section presenting the range of observed variation in size, form, color, vestiture, and secondary sexual characters. One sample of each sex is treated statistically in the manner described above. Geographic variation is not treated in depth in the present paper, although there are several groups that obviously require further study at this level (*Cis americanus*, page 444; *Cis creberrimus*, page 452; *Orthocis punctatus*, page 486).

Label Data and Collections

Because of the large numbers of specimens examined, complete label data are given only for the type series. In all other cases, localities are listed (alphabetically by states and provinces), collecting dates are excluded, and host data is summarized. Maps are also included for the majority of North American species. The summarization of host data is discussed on page 435. Sources of material (institutions and private collections) are also listed only for types. The following abbreviations are used in the text to refer to locations of types and paratypes: BMNH, British Museum (Natural History); BRUS, Institute Royale des Sciences de Belgique; CAS, California Academy of Sciences; CIN, Cincinnati Museum of Natural History; FMNH, Field Museum of Natural History; GEN, Muséum d'Histoire Naturelle, Geneva; JFC, J. F. Cornell Collection; JFL, J. F. Lawrence Collection; MCZ, Museum of Comparative Zoology; MNHN, Muséum National d'Histoire Naturelle, Paris; MZUH, Museum Zoologicum Universitatis Helsinki; PURD, Purdue University; UAZ, University of Arizona; USNM, United States National Museum; UW, University of Washington; UWS, University of Wisconsin.

SYSTEMATICS OF THE FAMILY CIIDAE

Historical Review

The earliest recognized name in the Ciidae is Scopoli's *Dermestes boleti*, but the genus *Cis* was not described by Latreille until 1796 and the family Ciidae (Cisidae) was proposed by Leach in 1819. The first world monograph of the family was that of Mellié (1848), which included 106 species in eight generic groups, and no other world study has been attempted since. Contributions made within the next eighty years consisted mainly of European faunal works (Thomson, 1863; Abeille de Perrin, 1874b; Kiesenwetter, 1877; Reitter, 1902a) and exotic faunal surveys resulting from foreign expeditions (Gorham, 1883, 1886; Scott, 1926). The Junk catalogue for the family (Dalla Torre, 1911) included 19 genera and 233 species. Outside of North America, most of the work on the family in the last forty years has concerned the Japanese fauna (Chujo, Miyatake, Nakane, Nobuchi) and the Pacific fauna (Blair and Zimmerman). In addition, Pic described almost 100 species from all over the world, and recently European workers, such as Lohse (1964–1969), have renewed interest in the Palaearctic Ciidae.

Although Mellié's monograph included several North American species and Mannerheim described a few from expeditions to Russian America, LeConte and Horn almost ignored the group, and the first major treatment in this country was that of Casey (1898), which included 8 genera and 44 species. Kraus (1908) and Blatchley (1910) added a few more forms, and in 1914 Dury published his North American synopsis that was meant to serve as a supplement to the earlier paper by Casey. Very little has been published since on the North American fauna, with the exception of Hatch's coverage in "Beetles of the Pacific Northwest" (1962) and my recent papers (Lawrence, 1965, 1967a, 1967b).

Family Limits

The composition of the family has varied over the years, and several forms have been removed to other groups. Two genera that are obviously not allied to the Ciidae are *Hendecatomus* Mellié and *Rhipidandrus* LeConte. The former was included in the family by most authors until Lesne (1934, 1935) presented considerable evidence for its removal to the Bostrichidae. The true relationships of *Hendecatomus* had been recognized much earlier, however, by Jacquelin du Val (1861) and LeConte (1861), and the latter had proposed the tribe Hendecatomini within the Bostrichidae. The genus *Rhipidandrus* was placed in the Ciidae by LeConte and Horn (1883), although it was originally described as a tenebrionid (LeConte, 1862) and has been treated as such by most workers (*see* Barber, 1913). In spite of the reduced tarsi (4–4–4) and pectinate antennae, there is little doubt that the group belongs in the Tenebrionidae and is probably related to the *Eledona* Latreille.

The genus *Pterogenius* Candeze is not as easily dispensed with. It was included in the family Ciidae until Crowson (1955) transferred it to a new family (Pterogeniidae) along with *Histanocerus* Motschulsky (= *Labidocera* Gebien). These two genera belong among the primitive Heteromera as defined by Crowson (1955, 1960, 1966, 1967) and are thus more or less closely related to the Ciidae; they differ from all ciid genera, however, in a number of characters, including the following: 1) antennae 11-segmented, filiform or gradually enlarged apically, without sensillifers; 2) maxillary palps securiform; 3) tarsal formula 5–5–4; 4) procoxal cavities closed internally; 5) mesotrochantins visible; 6) abdominal sternites III and IV connate; 7) anal region of hindwing with four veins, the anterior one running through the subcubital fleck, and a wedge cell. It is unlikely that this family represents the sister group of the Ciidae, but it must be taken into consideration in any study of the primitive heteromerous Coleoptera (Crowson, 1966).

Another genus doubtfully included in the Ciidae is *Sphindocis* Fall (1917), described on the basis of a single species, *S. denticollis,* from coastal California. The beetle has been collected at various localities from Alameda County to northern Mendocino County and is usually found breeding in the fruiting bodies of *Trametes sepium* growing on dead and fallen branches of Madrone (*Arbutus Menziesii*). The adult of *Sphindocis* resembles a large *Orthocis* and exhibits the following similarities to members of the Ciidae: 1) procoxae without lateral extensions, trochantin hidden; 2) procoxal cavities open internally and posteriorly; 3) mesepimera reaching mesocoxal cavities; 4) hindwing with subcubital fleck; 5) abdominal sternite III in male with pubescent fovea; 6) tarsal formula 4–4–4 in both sexes; 7) aedeagus of inverted heteromeroid type. The *Sphindocis* larva is similar to a ciid larva in general form (see below), and the mouthparts do not differ from those of a ciid larva in any significant manner. Tergite IX is modified to form a sclerotized, concave disc, similar to that found in *Cis melliei* Coquerel (1849) and in the tenebrionid *Meracantha contracta* (Beauvois) (Hyslop, 1915). A number of these adult and larval features may be found in other Cucujoidea, however, and the differences presented in Table 1 argue for the exclusion of the genus from the Ciidae. Crowson (*in litt.*) has suggested that *Sphindocis* may represent the sister group of the Ciidae proper and that both groups might be included in one family. I think it is just as likely that the former is allied to the Tetratomidae or Prostomidae (see below) and I prefer to exclude it in the present treatment.

Characterization of the Family Ciidae

The following description will serve to distinguish members of this family from

Table 1. Differences between *Sphindocis* and the Ciidae

Characters	Sphindocis	Ciidae
Antenna	no sensillifers 11-segmented	8- to 10-segmented with sensillifers
Maxilla	with 2 well-developed lobes	with reduced lacinia
Mesotrochantin	visible	not visible
Metendosternite	With median stalk	without median stalk
Anal region of hindwing	with 4 veins and wedge cell; subcubital fleck undivided	with 1 vein; subcubital fleck divided
Abdominal sternites III and IV	connate	free
Trochanters	heteromeroid type	normal type
Tibial spurs	present	absent
Basal piece of aedeagus	large with 2 condyles	small, without condyles
Median lobe of aedeagus	membranous with lateral struts	sclerotized
Larval spiracle	biforous	annular
Larval antenna	3-segmented	2-segmented
Larval sternite IX	with row of asperites	without asperites

all other Coleoptera. A more complete comparative study of adults and larvae will be the subject of a paper in preparation.

With the general characters of the Polyphaga: Cucujoidea.

Adult. Form variable, usually oval to elongate, convex. Size 0.5–6.0 mm.

Head globular, without neck, declined, often strongly so, partly concealed by pronotum. Eye somewhat protuberant, oval, entire, fairly coarsely faceted. Frontoclypeal area with distinct suture, often raised in males to form a ridge. Antennal insertion in fossa formed by genal ridge and eye, concealed from above by frons. Antenna 8- to 10-segmented, with large pedicel and scape and 2- or 3-segmented club, each club segment bearing at least 4 sensillifers at apex. Mandible bidentate, with simple molar area. Maxilla with galea and lacinia reduced, palp 4-segmented with terminal segment subconical, not securiform. Labium with ligula absent, palp 3-segmented.

Pronotum margined laterally and posteriorly, anterior edge usually produced forward. Prosternum variable, long or short, concave to carinate, coxae globose or transverse, sometimes projecting, contiguous to broadly separated, without internalized lateral extensions, trochantin hidden. Procoxal cavities open internally, narrowly open or closed posteriorly.

Elytra not striate, humeri tuberculate, epipleurae very narrow, extending almost

to apex. Scutellum small and subtriangular. Wing venation reduced, with 1 anal vein (or none); subcubital fleck present, divided.

Mesosternum short, coxae globose and narrowly separated, coxal cavities not closed outwardly by sterna, trochantins hidden. Metasternum subquadrate, with or without median suture, coxae narrow, transverse, subcontiguous. Metendosternite consisting of a pair of diverging arms with anterior tendons near apices.

Tarsal formula in both sexes 4–4–4 (occasionally 3–3–3). Tarsi simple, first 3 segments small and subequal, terminal segment elongate, claws simple. Trochanters oblique, normal type (completely separating coxa from femur). Tibiae without apical spurs, outer edge of protibia often expanded and modified at apex.

Abdominal segments all freely articulated, first segment without coxal lines, often with a median pubescent fovea in male. Aedeagus of inverted heteromeroid type, with small basal piece, ventral tegmen, and dorsal median lobe.

Larva. Orthosomatic, without lateral extensions, lightly and evenly sclerotized except for head, thoracic tergite I, and abdominal tergite IX (occasionally VIII). Head with Y-shaped epicranial suture, 5 ocelli or less, and short gula. Antenna 2-segmented, second segment bearing a long, ventral, sensory appendage near base and a long seta at apex. Mandible bidentate, with or without "retinaculum," with or without molar area. Maxilla with obliquely obtuse mala and a small, dorsal, subapical lobelike lacinia. Spiracles small, annular. Two setae on claw. Tergite IX variously armed but usually bearing 2 "urogomphi"; sternite IX without asperites. Segment X pygopodlike.

Phylogenetic Relationships

The placement of the Ciidae within the order Coleoptera has a complex history, and the group has been associated at various times with the Bostrichoidea, Cleroidea, Clavicornia, and Heteromera. In the 19th Century, the family was commonly placed with the Bostrichidae and their allies (Teredilia, Xylophages, Bostrichoidea) primarily on the basis of the cylindrical form, declined head, expanded and often spinose tibiae, and other features associated with the boring habit. Casey (1890) considered the group to comprise a subfamily of the Cryptophagidae, which was used in a very broad sense to include the Mycetophagidae, Sphindidae, and Biphyllidae as well.

Forbes (1926) united the Ciidae with the Lathridiidae, Corylophidae, and Murmidiidae (= Cerylonidae) on the basis of wing venation and folding, and he derived this group of families from the Endomychidae and Colydiidae partly on the basis of the "double chitinization" in the anal region of the wing. This anal chitinization refers to the subcubital fleck of Crowson (1955), which is found in a number of cucujiform families and which may be divided by the first anal vein and remains divided even after the vein has been lost. A divided subcubital fleck occurs in several families, including the Endomychidae, Lathridiidae, Biphyllidae, Byturidae, Colydiidae, Pterogeniidae, and Ciidae. An undivided fleck occurs in the Mycetophagidae, Tetratomidae, *Sphindocis*, Salpingidae, and several other groups (Bernet-Kempers, 1923; Crowson, 1955; Forbes, 1926; Miyatake, 1960; Wilson, 1930). A further study of this character (whose function is at present unknown) may shed some light on relationships among the Cucujoidea.

Böving and Craighead (1930, 1931) included the Ciidae in the Cleroidea on the basis of larval characters, such as the lack of a mandibular mola (actually present in some Ciidae) and the reduction of the maxillary articulating area (also occurring in some cucujoids), while Jeannel and Paulian (1944) related the family to the Colydiidae, Byturidae, Boridae, and several other families on the basis of male genitalia.

Crowson (1955) presented convincing evidence for excluding the Ciidae from the Bostrichoidea and Cleroidea but expressed doubt as to the affinities of the group within the Cucujoidea. In later works (1960, 1966, 1967), Crowson placed the Ciidae within the section Heteromera and indicated possible relationships to several of the more primitive families, such as the Biphyllidae, Byturidae, Mycetophagidae, Pterogeniidae, Tetratomidae, Prostomidae, and Colydiidae.

I agree basically with Crowson's view that the Ciidae are primitive members of the Heteromera, but the affinities of the group to other heteromerous families are not at all clear, and the possibility still exists that they have been derived independently from some clavicorn stock, such as the Languriidae. The prothoracic structure resembles that of the Mycetophagidae, Tetratomidae, and *Sphindocis,* in that the coxae are not internalized (lacking lateral extensions) and the cavities are open internally and posteriorly. Other primitive heteromeran characters include the free abdominal sternites, nonheteromeroid trochanters, and annular larval spiracles. Specialized features, such as the reduction of antennal segments, maxillary lacinia, tarsi, and anal region of hindwing, and the loss of tibial spurs and the median stalk of the metendosternite all may be correlated with size decrease. The pygopodlike 10th abdominal segment in the larva occurs in both the Clavicornia and Heteromera and may be associated with the habit of boring into fungi.

As mentioned above, the Ciidae, *Sphindocis,* and the Pterogeniidae are similar in several respects. In all three, the procoxae are not internalized, the aedeagus is of the inverted heteromeroid type, and the larval mouthparts are similar, the maxilla, for instance, possessing a distinct laciniar lobe. In *Sphindocis,* however, the 9th larval ventrite bears a row of asperites, the antennae are 11-segmented without sensillifers on the club, the trochanters are heteromeroid, and the subcubital fleck is not divided; in the Pterogeniidae, the procoxal cavities are internally closed, the antennae are filiform, the tarsal formula is 5–5–4, and the maxillary palps are strongly securiform; while in both of the latter groups, the larval spiracles are biforous, the first two abdominal sternites are connate, tibial spurs are present, and the mesotrochantins are visible. *Sphindocis* appears to be more closely related to the Tetratomidae and Mycetophagidae, while the Pterogeniidae may have affinities with the Neotropical genus *Ischyomius* or perhaps to the byturid-biphyllid group.

Other primitive heteromerous families with which the Ciidae might be associated are the Byturidae, Biphyllidae, Prostomidae, Colydiidae, and perhaps the Tenebrionidae and their close allies. It is also possible that the Heteromera, as it is now constituted, does not represent a monophyletic group, in which case certain of the more primitive forms might be derived independently from different clavicorn ancestors. The wing venation in the ciids is similar to that of certain cerylonoid groups, such as the Lathridiidae and Endomychidae, while antennal sensillifers are found in the languriid genus *Cryptophilus* and the overall adult structure in the Ciidae is closely approached in another languriid genus *Setariola.* Similar wing venation (with divided subcubital fleck) may also be found in the heteromerous Colydiidae, however, and antennal sensillifers occur in *Myrmechixenus* (Colydiidae?) and *Szekessya* (Prostomidae?), as well as in a variety of true Tenebrionidae.

The position of the family Ciidae must remain in doubt for the present, until a thorough phylogenetic study of the primitive Heteromera is completed. The phylogenetic relationships within the family Ciidae are also unclear and will not be discussed in detail here. The basic division into subfamilies appears to be sound, and the prothoracic differences used in the

TABLE 2. DISTRIBUTIONAL PATTERNS OF FAUNAL AFFINITIES OF NORTH AMERICAN CIIDAE.

Ciid species	NW	NE	SE	SW	Faunal affinities
CIS					
acritus	x			xx	Neotropical?
americanus	xx	x	x		Palaearctic?
angustus	xx				Palaearctic
biarmatus	xx				Palaearctic
castlei		x	xx		Neotropical
cayensis			xx		Neotropical (1)
congestus		x	xx		Neotropical
cornelli			xx		Neotropical
cornutus		x	xx		Neotropical
creberrimus		x	xx	x	Neotropical
crinitus			xx		Neotropical (1)
discolor				xx	Neotropical (2)
dunedinensis			xx		Neotropical (1)
duplex				xx	Neotropical (2)
ephippiatus	xx	x			Palaearctic
festivulus		xx			Palaearctic
floridae			xx		Neotropical (1)
fuscipes	x	x	x		Palaearctic
hirsutus			xx		Neotropical (1)
horridulus	x	xx	x	x	Palaearctic
huachucae			x	xx	Neotropical
hystriculus	xx				Palaearctic
krausi			xx		Neotropical (1)
laminatus		(xx)			Palaearctic
levettei	x	xx	x		Palaearctic
maritimus	xx	x			Palaearctic
megastictus	xx				Palaearctic
miles		x	xx		Neotropical
niedhauki			xx		Neotropical (1)
pistoria	x	xx			Palaearctic
quadridentatus		x	xx		Oriental?
robiniophilus		xx			Palaearctic
rotundulus			xx		Neotropical (1)
stereophilus		x	xx		Neotropical
striolatus	x	xx	x		Palaearctic
subfuscus			xx		Neotropical
subtilis		x	xx		Neotropical?
tetracentrum				xx	Neotropical
tridentatus	xx				Palaearctic?
tristis		x	xx		Neotropical?
ursulinus		x	xx		Neotropical (1)
versicolor	x			xx	Neotropical
vitulus	xx			x	Neotropical
ENNEARTHRON					
aurisquamosum		x	xx		Oriental?
spenceri	(xx)				Palaearctic
DOLICHOCIS					
indistinctus	xx	x		x	Palaearctic
manitoba	xx	x			—
ORTHOCIS					
huesanus			xx		Neotropical
longulus		x	xx		Neotropical
pulcher			xx		Neotropical (1)

Table 2. (Continued)

Ciid species	NW	NE	SE	SW	Faunal affinities
ORTHOCIS (Continued)					
punctatus	x	xx	x	x	Palaearctic
transversatus			xx		Neotropical (1)
STRIGOCIS					
bilimeki				(xx)	Neotropical (2)
opacicollis		x	xx		Neotropical (2)
opalescens		x	xx		Neotropical (2)
HADRAULE					
blaisdelli	x	x		xx	——
elongatula		(xx)			Palaearctic
explanata		xx			Palaearctic
PLESIOCIS					
cribrum	xx	x		x	——
CERACIS					
californicus	x	x		xx	Neotropical
curtus		x	xx		Neotropical (1)
dixiensis	x			xx	Neotropical
magister			xx		Neotropical
minutissimus		x	xx		——
minutus			xx		Neotropical (1)
monocerus			xx		Neotropical
multipunctatus			xx		Neotropical (1)
nigropunctatus			xx		Neotropical
obrieni				xx	Neotropical
pecki		x	xx		Neotropical
powelli				xx	Neotropical (2)
pullulus			xx		Neotropical (1)
punctulatus		x	xx		Neotropical (1)
quadricornis			xx		Neotropical
sallei		x	xx		——
schaefferi			xx		Neotropical
similis				(xx)	Neotropical
singularis		x	xx		Neotropical
thoracicornis		x	xx		——
SULCACIS					
curtulus	xx	x	x	x	Palaearctic
lengi		x	xx		——
MALACOCIS					
brevicollis		x	xx		Neotropical
RHOPALODONTUS					
americanus		xx			Palaearctic
OCTOTEMNUS					
laevis	x	xx	x		Palaearctic

key (p. 436) are correlated with a number of other characters. The Orophiinae contains several distinct genera, while the much larger Ciinae requires considerable revision. It is hoped that an improved generic classification, based on larval and adult characters, will result from a study now in progress.

TABLE 3. COMPARISON OF FAUNAL SECTORS.

	NW		NE		SE		SW		NW
Total species	26		45		53		20		26
Indigenous species	15		10		44		13		15
Endemic species	6		6		21		7		6
Shared species		16		29		5		11	
S. C.		61.5		64.4		25.0		55.0	

Family Name

The spelling of the family name has been a subject of controversy for many years. The family was originally named Cisidae by Leach (1819), and Wollaston (1854) used Cissidae. Gistel (1856) appears to be the first to use Cioidae, and this spelling was used by most German authors (Kiesenwetter, 1877; Reitter, 1902a) until recently. Ciidae was first used by Marseul (1887) and has been adopted by a number of recent workers. The type genus *Cis* is derived from the Greek masculine noun *kis, kios,* meaning a worm which bores into wood. The genitive stem is *ki-*, so that the correct family name should be Ciidae. There is no doubt that Ciidae is the correct spelling, but Grensted (1940, 1947) has suggested that this name be replaced by one that is more euphonious and more clearly linked to the genus name *Cis*. Among recent authors, Arnett (1962), Crowson (1955), and Lohse (1967) have all used Cisidae, while I have continued to use Ciidae, as have Miyatake (1954) and other Japanese workers. This is a relatively unimportant matter and is included here only to clarify the inconsistent spellings found in the literature.

THE NORTH AMERICAN CIIDAE

The family Ciidae in North America includes 12 genera and 84 species, 16 of which are here described as new. The majority of species fall into the two genera *Cis* (43) and *Ceracis* (20), while most of the genera are represented by one or two species only.

Origin and Distribution

As would be expected the major affinities of the North American ciids are with the Neotropical and Palaearctic faunas. One or two species may be related to Oriental forms, but there is no evidence for Ethiopian or Australian affinities. A general faunistic analysis of the North American species is presented in Tables 2 and 3. The continent has been divided into four sectors, as shown in Figure 87, and in Table 2 the occurrence of a ciid species within a sector is indicated by an "x," while an "xx" is used for the sector in which the species is assumed to be indigenous (or at least most common and widespread relative to the remainder of the area considered). Doubtful occurrences or possible introductions are indicated by "(xx)." Finally, the last column gives the zoogeographic region in which the closest relatives of the species occur. The number (1) after Neotropical indicates West Indies, while the number (2) stands for the Mexican Plateau. Table 3 gives the total species, indigenous species, and endemic species for each sector and an expression of faunal similarity between each adjacent sector, using Simpson's Coefficient (Simpson, 1947; S. C. = $100C/n_1$, where C is the number of species common to the two faunas and n_1 the number of species in the smaller fauna). This is a very coarse analysis, since relatively broad and arbitrary sectors have been chosen, but it will serve to emphasize some of the major features of ciid distribution in North America.

A more relevant type of distributional study is one which takes into consideration geographical origins and phylogenetic affinities, such as that of Linsley (1958) on the Cerambycidae. Since the Ciidae are

associated with woody plants, as are the cerambycids, it would be useful to compare Linsley's faunal elements with those based on the Ciidae. The North American ciids are most easily grouped into three major faunas, one of which may be further divided into three subfaunas. These are discussed below.

Northern fauna. This includes 26 species which occur, for the most part, in the northern forests and mountainous regions of North America, and are usually allied to forms from northern Eurasia.

Cis americanus	*Cis robiniophilus*
Cis angustus	*Cis striolatus*
Cis biarmatus	*Cis tridentatus*
Cis ephippiatus	*Enn. spenceri*
Cis festivulus	*Dol. indistinctus*
Cis fuscipes	*Dol. manitoba*
Cis horridulus	*Orth. punctatus*
Cis hystriculus	*Hadr. elongatula*
Cis laminatus	*Hadr. explanata*
Cis levettei	*Ples. cribrum*
Cis maritimus	*Sulc. curtulus*
Cis megastictus	*Rhop. americanus*
Cis pistoria	*Oct. laevis*

Some of these species are equally common in the Northeast and Northwest (*O. laevis*, Fig. 109), others may be common in the western forests but rare in the Northeast (*P. cribrum*, Fig. 89), and still others are restricted to the Northwest Coast (*C. biarmatus*, Fig. 102). Some forms occur in association with hardwoods (*S. curtulus*, *C. fuscipes*, *O. laevis*, and *C. pistoria*), and others are found on conifers (*C. biarmatus*, *P. cribrum*, and *C. hystriculus*), but the majority may be found on either. Most of the species comprising this fauna would form part of the modern Holarctic element of Linsley and are related to or even synonymous with northern Palaearctic forms. The following species pairs (Nearctic-Palaearctic) are very closely allied and some may be conspecific: *Cis horridulus-C. tomentosus* Mellié; *Cis hystriculus-C. punctulatus* Gyllenhal; *Cis levettei-C. glabratus* Mellié; *Cis pistoria-C. micans* (Fabricius); *Cis striolatus-C. striatulus* Mellié; *Dolichocis indistinctus-D. laricinus* (Mellié); *Orthocis punctatus-O. alni* (Gyllenhal); *Sulcacis curtulus-S. bidentulus* (Rosenhauer); *Rhopalodontus americanus-R. strandi* Lohse; *Octotemnus laevis-O. glabriculus* (Gyllenhal). Three of these northern species (*Cis laminatus*, *Ennearthron spenceri*, and *Hadraule elongatula*) may represent recent introductions. Two species, *Cis festivulus* and *C. robiniophilus*, also have Palaearctic counterparts —*C. festivus* (Panzer) and *C. castaneus* Mellié, respectively—but are more southern in distribution and may represent an older element which Linsley called the Alleghenian. In Western North America, there are several coastal forms (*Cis angustus*, *C. biarmatus*, *C. ephippiatus*, *C. maritimus*, *C. megastictus*, and *C. tridentatus*) which do not have Palaearctic near relatives, but which belong to Holarctic species groups. These may be part of the Vancouveran of Linsley, in that their Old World affinities are not as close. Finally the two species *Dolichocis manitoba* and *Plesiocis cribrum* appear to be the most isolated forms with no obviously related species in the Old World or in the Neotropical Region.

Southwestern fauna. This group includes 15 species (one of which is also mentioned in the next section), which would form part of the Sonoran and Californian faunas of Linsley. Their ranges extend from northern California through the Southwest into Mexico.

Cis acritus	*Cis vitulus*
Cis creberrimus	*Str. bilimeki*
Cis discolor	*Hadr. blaisdelli*
Cis duplex	*Cer. californicus*
Cis huachucae	*Cer. dixiensis*
Cis tetracentrum	*Cer. obrieni*
Cis versicolor	*Cer. powelli*
	Cer. similis

Only four of the above species occur in central and northern California, while the

remainder are restricted to the Southwest. *Cis vitulus* is practically restricted to California, occurs in mesic and humid habitats, and is most closely related to *Cis congestus* of the Southeast and to several Neotropical species; this is the only species that I would consider part of Linsley's Californian subfauna. *Cis versicolor, Hadraule blaisdelli,* and *Ceracis californicus* extend north along the Pacific Coast, but are also common in the Southwest at low and intermediate elevations. *Cis acritus, C. creberrimus, C. discolor, C. duplex,* and *Ceracis powelli* are usually found in coniferous forests at higher elevations, while *Cis tetracentrum* occurs in mountain canyons, along with *Cis versicolor, Ceracis californicus,* and *Ceracis dixiensis.* The last three species also inhabit the arid lowlands, as do *Ceracis obrieni* and probably *Ceracis similis.*

Southeastern fauna. This includes the great majority of North American Ciidae occurring east of the 100th Meridian and corresponds, for the most part, to Linsley's Neotropical Fauna. It may be subdivided into three groups: 1) the main group of species ranging from New England and the Great Lakes south to Florida and Texas, 2) the Antillean group occurring mainly in Florida and adjacent states, and 3) the Mexican group extending into southern Texas and along the Gulf Coast to Louisiana. These will be discussed separately below.

1) Main group (24 species).

Cis castlei	*Enn. aurisquamosum*
Cis congestus	*Orth. longulus*
Cis cornelli	*Str. opacicollis*
Cis cornutus	*Str. opalescens*
Cis creberrimus	*Cer. minutissimus*
Cis miles	*Cer. pecki*
Cis quadridentatus	*Cer. punctulatus*
Cis rotundulus	*Cer. sallei*
Cis stereophilus	*Cer. singularis*
Cis subtilis	*Cer. thoracicornis*
Cis tristis	*Sulc. lengi*
Cis ursulinus	*Mal. brevicollis*

Most of the species in this group have Neotropical affinities and the ranges of many extend into northern Mexico. Those with continuous distributions into Mexico (usually somewhat broken up in the more arid regions) are probably more modern Neotropical elements, while those with more restricted southeastern distributions may represent older Alleghenian forms. *Cis congestus* (Fig. 105), with its counterpart *C. vitulus* in California, is probably one of the latter, while *Ennearthron aurisquamosum* represents an Alleghenian species with Old World affinities, its closest relative occurring in southwestern China. *Cis quadridentatus* is a rather widespread form and its relationships are obscure; it may be related to an Oriental group of species. *Cis rotundulus* and *C. ursulinus* belong to a West Indian species group, but they appear to have evolved on the mainland and are more widespread than the Antillean forms discussed below (Figs. 89 and 92).

2) Antillean group (16 species).

Cis cayensis	*Orth. pulcher*
Cis crinitus	*Orth. transversatus*
Cis dunedinensis	*Cer. curtus*
Cis floridae	*Cer. magister*
Cis hirsutus	*Cer. minutus*
Cis krausi	*Cer. monocerus*
Cis niedhauki	*Cer. multipunctatus*
Orth. huesanus	*Cer. pullulus*

Most of the species in this group occur only in southern Florida and the majority are also found in the Greater Antilles. *Cis krausi* and *Orthocis transversatus* also occur in Texas and might be included in the next group, but both have close relatives in the West Indies.

3) Mexican group (4 species). *Cis subfuscus, Ceracis nigropunctatus, Ceracis quadricornis,* and *Ceracis schaefferi* are Neotropical species that occur in Texas and Mexico but are not found in the West Indies. There are probably several more undescribed forms that extend into southern

Texas, but the fauna of that region is not well known at present.

Host Preference

The subject of host preference or specificity in the North American Ciidae has been discussed briefly in a previous paper (Lawrence, 1967b) and will be covered in detail in a future publication (Lawrence, in press).

More than 100 species of fungi have been recorded as ciid hosts in North America, and the great majority of these belong to the basidiomycete family Polyporaceae. In the following text, all host records are listed for each ciid species. For each fungus, the total number of records and the number of "breeding" records (in parentheses) are given. A particular record is considered to be a breeding record if it consists of any one of the following: 1) ten or more fully pigmented adults, 2) two or more tenerals only, 3) one teneral and two or more fully pigmented adults, or 4) one or more larvae and/or pupae. Species of fungi are listed according to the number of records, so that preferred hosts are first. An example is as follows: *Polyporus anceps* [6(5)]; *Fomes officinalis* [2(2)]; *Fomes pinicola* [2(2)]; *Ganoderma oregonense* [1(1)]. The classification of fungi used in the presentation of host data is a rather conservative one, following Lowe (1957, 1966), Lowe and Gilbertson (1961a, 1961b), and Overholts (1953).

Patterns of host preference have been demonstrated for British Ciidae (Paviour-Smith, 1960, 1969) and for North American *Ceracis* (Lawrence, 1967b). The following is a preliminary grouping of 58 North American ciids into the four host preference groups discussed in the *Ceracis* paper. A detailed analysis of host data will be presented at a later date (Lawrence, in preparation).

Polyporus versicolor group. Fungi with thin, whitish, coriaceous fruiting bodies and trimitic hyphal system (*Polyporus versicolor*, *P. hirsutus*, *Lenzites betulina*, *Trametes hispida*, etc.).

Cis congestus	*Str. bilimeki*
Cis cornutus	*Str. opacicollis*
Cis fuscipes	*Str. opalescens*
Cis miles	*Cer. dixiensis*
Cis pistoria	*Cer. minutus*
Cis subfuscus	*Cer. quadricornis*
Cis tetracentrum	*Cer. monocerus*
Cis tristis	*Sulc. curtulus*
Cis versicolor	*Sulc. lengi*
Cis vitulus	*Oct. laevis*

Polyporus pargamenus group. Fungi similar to the above but with brownish or purple pore surface (*Polyporus abietinus*, *P. pargamenus*, *P. sector*, *Daedalea unicolor*).

Cis acritus	*Cis subtilis*
Cis horridulus	*Cer. minutissimus*
Cis hystriculus	*Cer. powelli*
Cis striolatus	*Cer. thoracicornis*

Polyporus gilvus group. Fungi with woody or fibrous fruiting bodies, brownish in color and turning black in potassium hydroxide, dimitic or monomitic hyphal system (*Polyporus gilvus*, *P. licnoides*, *Fomes igniarius*, *F. robiniae*, etc.).

Cis cayensis	*Cer. pecki*
Cis maritimus	*Cer. pullulus*
Cis niedhauki	*Cer. punctulatus*
Cer. magister	*Cer. singularis*
Cer. obrieni	*Mal. brevicollis*

Ganoderma applanatum group. Diverse fungi with dark or light tissues and dimitic or trimitic hyphal systems (*Ganoderma applanatum*, *G. lucidum*, *Fomes fomentarius*, *F. pinicola*, *Polyporus betulinus*, *P. adustus*, *P. hydnoides*, etc.).

Cis americanus	*Dol. indistinctus*
Cis angustus	*Dol. manitoba*
Cis biarmatus	*Cer. californicus*
Cis castlei	*Cer. curtus*
Cis creberrimus	*Cer. multipunctatus*
Cis ephippiatus	*Cer. nigropunctatus*
Cis hirsutus	*Cer. sallei*

Cis levettei	*Cer. schaefferi*
Cis megastictus	*Cer. similis*
Cis tridentatus	*Rhop. americanus*

Some Ciidae are restricted to fungi not included in the above groups. *Plesiocis cribrum,* for instance, is almost always found in the fruiting bodies of *Polyporus volvatus,* while *Cis stereophilus* prefers those of thelephoraceous fungi in the genus *Stereum.* Within the above groups (especially the last) the preferences of individual species vary considerably and some (*Cis americanus*) have a much wider host range than others (*Cis ephippiatus, Ceracis sallei*). Further details on host specificity will be included in species discussions.

Key to the Subfamilies and Genera of North American Ciidae

1. Procoxae subconical, strongly projecting below intercoxal process, which does not extend to middle of coxae (Figs. 16 and 25); metasternal suture absent (Fig. 33); first visible abdominal sternite (III) in male with posteriorly projecting, triangular flap, which partly conceals pubescent fovea (Fig. 31) .... Orophiinae 2

— Procoxae transverse or globular, not projecting below intercoxal process, which extends beyond middle of coxae (Figs. 17, 22–24, 26–28); metasternal suture present (Fig. 34); first visible abdominal sternite in male simple or foveate, but without triangular flap (Fig. 32) .... Ciinae 3

2. Outer edges of all tibiae spinose for more than one-third of their lengths (Fig. 60); antennae 8-segmented; body form oval; vestiture consisting of minute hairs, which are not visible under 10× magnification, and a few scattered long, fine hairs; pronotal punctation finer and sparser, the punctures much smaller than those on elytra and separated by 1.5 diameters or more .... *Octotemnus* (p. 508)

— Outer edges of tibiae with spines at apex only (Fig. 59); antennae 10-segmented; body form cylindrical; vestiture consisting of long, fine hairs; pronotal punctation coarser and denser, the punctures slightly smaller than those on elytra and usually separated by less than 1.0 diameter .... *Rhopalodontus* (p. 506)

3. Prosternum in front of coxae almost twice as long as intercoxal process (Fig. 28); sides of pronotum subparallel or slightly diverging towards apex (Figs. 20–21, 28); body small, elongate, and extremely flattened, TL usually less than 1.4 mm.; EL/EW greater than 1.60, and GD/EW usually less than 0.65; antennae 9-segmented with a 2- or 3-segmented club; elytral punctation dual and distinctly seriate, micropunctures bearing short, fine hairs or bristles .... *Hadraule* (p. 491)

— Prosternum in front of coxae not or slightly longer than intercoxal process; without other characters in combination 4

4. Outer apical angle of protibia expanded, rounded, and bearing several spines (Figs. 57–58) 5

— Outer apical angle of protibia not as above, usually produced and dentate (Figs. 49–51, 54–56), blunt and angulate (Figs. 52–53), or narrowly rounded (Figs. 45–47); if expanded and rounded, then not spinose (Fig. 48) 8

5. Prosternum in front of coxae carinate and on same plane as intercoxal process (Figs. 13–14); lateral edges of pronotum visible for their entire lengths from above; anterior pronotal angles slightly produced (Fig. 14); elytral suture with inflexed margin near apex (Fig. 38); antennae 10-segmented .... *Strigocis* (p. 488)

— Prosternum in front of coxae concave or biconcave and on different plane than intercoxal process (Figs. 9–10, 15); lateral edges of pronotum not visible for their entire lengths from above; anterior pronotal angles rounded or obtusely angulate, not produced (Fig. 15); elytral suture without inflexed margin near apex 6

6. Intercoxal process of prosternum laminate, less than 0.15 × as wide as a procoxal cavity (Fig. 24); vestiture consisting of very short, fine hairs; pronotum of male usually bearing tubercles, horns, or laminae at apex; antennae 8- to 10-segmented .... *Ceracis* (p. 494)

— Intercoxal process of prosternum not laminate, at least 0.20 × as wide as a procoxal cavity (Fig. 27); vestiture consisting of short, stout bristles; pronotum of male always simple 7

7. Pronotum very short and broad, PL/PW less than 0.73; prosternum in front of coxae only half as long as intercoxal process (Fig. 27); metasternum at midline less than 0.40 × as long as broad; antennae 10-segmented in North American species .... *Malacocis* (p. 504)

— Pronotum more elongate, PL/PW more than 0.73; prosternum in front of coxae not or only slightly shorter than intercoxal proc-

ess; metasternum at midline more than 0.40 × as long as broad; antennae 9- or 10-segmented .... *Sulcacis* (p. 502)

8. Outer apical angle of protibia narrowly rounded (Fig. 45); elytral suture with an inflexed margin near apex (Fig. 38); head and pronotum in both sexes without tubercles or horns, male sometimes with densely pubescent area on clypeus (Fig. 37); elytral punctation single and uniform; vestiture consisting of very short, fine hairs; body elongate and parallel-sided, antennae 9- or 10-segmented .... *Orthocis* (p. 484)

— Outer apical angle of protibia usually produced and dentate or blunt and angulate, if somewhat rounded, then vestiture consisting of short, stout bristles or elytral punctation dual and head of male bearing horns or tubercles; elytral suture without inflexed margin 9

9. Antennae 10-segmented .... *Cis* (p. 437)

— Antennae 9-segmented 10

10. Outer apical angle of protibia rounded (Fig. 46); body more elongate, EL/EW usually more than 1.50; apex of pronotum simple in both sexes .... *Dolichocis* (p. 482)

— Outer apical angle of protibia produced and dentate; body shorter and broader, EL/EW usually less than 1.50; apex of pronotum in male produced and emarginate forming 2 horns or tubercles (Figs. 4 and 8) 11

11. Intercoxal process of prosternum less than 0.25 × as wide as a procoxal cavity; metasternal suture less than 0.25 × as long as median length of metasternum; frontoclypeal ridge in male bearing 4 sharp teeth (Fig. 4) .... *Plesiocis* (p. 493)

— Intercoxal process of prosternum more than 0.25 × as wide as a procoxal cavity; metasternal suture more than 0.25 × as long as median length of metasternum; frontoclypeal ridge in male bearing 2 subtriangular plates with a distinct notch between them (Fig. 8) .... *Ennearthron* (p. 480)

Subfamily Ciinae

Cisidae Leach, 1819: 206.
Cissidae Wollaston, 1854: 279.
Cioidae Gistel, 1856: 143.
Ciidae Marseul, 1887: 293.

Included genera. All those not placed in the Orophiinae (p. 506). About 30 genera have been described, but a number of these will have to be synonymized and several remain to be described.

Genus *Cis* Latreille

Cis Latreille, 1796: 50; Latreille, 1802: 205; Gyllenhal, 1813: 377; Gyllenhal, 1827: 624; Redtenbacher, 1847: 348; Mellié, 1848: 236; Lacordaire, 1857: 551; Jacquelin du Val, 1861: 237; Thomson, 1863: 183; Abeille de Perrin, 1874b: 19; Kiesenwetter, 1877: 173; LeConte and Horn, 1883: 232; Casey, 1898: 78; Reitter, 1902a: 47; Blatchley, 1910: 897; Dalla Torre, 1911: 5; Leng, 1920: 246; Arnett, 1962: 829. Type species, by subsequent monotypy, *Dermestes boleti* Scopoli, 1763: 17 (Latreille, 1802: 205).

Eridaulus Thomson, 1863: 191; Lawrence, 1965: 282 (complete synonymy); Lawrence, 1967b: 98. Type species, by present designation, *Anobium nitidum* Fabricius, 1792: 238.

Xestocis Casey, 1898: 85; Lawrence, 1965: 282. Type species, by subsequent designation, *Xestocis levettei* Casey, 1898: 85 (Lawrence, 1965: 282).

Macrocis Reitter, 1878c: 34; Gorham, 1883: 219. Type species, by present designation, *Macrocis taurus* Reitter, 1878c: 34. NEW SYNONYMY.

Included species and species groups. This genus contains about 350 named species, which will not be listed here, and numerous undescribed forms as well. Some distantly related forms with 10-segmented antennae have been described as *Cis*, but even when these are eventually removed, the genus will be by far the largest in the family. Within the genus *Cis* there are a number of well-defined subgroups of varying size, the species of which usually have similar body form, male genitalia, secondary sexual characters, larval urogomphi, and food preferences. Several of the more obvious species groups are listed below, with the distribution, a few representative species, and all of the North American members. Of the 24 species groups listed, 6 are entirely exotic and the other 18 contain 34 of the 43 North American *Cis*.

C. bilamellatus group. Oriental-Australian. *C. bilamellatus* Wood, *C. australis* Blackburn, *C. clarki* Blair. North America: none.

C. boleti group. Holarctic. *C. boleti* (Scopoli), *C. rugulosus* Mellié, *C. micans* (Fabricius), *C. villosulus* (Marsham). North America: *C. pistoria* Casey.

C. cayensis group. Neotropical. North America: *C. cayensis,* n. sp., *C. niedhauki,* n. sp.

C. compressicornis group. Australian. *C. compressicornis* Fairmaire, *C. cervus* Blair. North America: none.

C. comptus group. Holarctic. *C. comptus* Gyllenhal, *C. striatulus* Mellié. North America: *C. striolatus* Casey, *C. versicolor* Casey?

C. creberrimus group. Nearctic-Neotropical. North America: *C. creberrimus* Mellié.

C. fagi group. Holarctic. *C. fagi* Waltl, *C. castaneus* Mellié. North America: *C. angustus* Hatch, *C. robiniophilus,* n. sp.

C. festivus group. Holarctic. *C. festivus* (Panzer), *C. pygmaeus* (Marsham), *C. vestitus* Mellié. North America: *C. festivulus,* n. sp.

C. fuscipes group. Holarctic-Oriental. *C. seriatopilosus* Motschulsky, *C. seriatulus* Kiesenwetter, *C. taiwanus* Chujo. North America: *C. fuscipes* Mellié.

C. huachucae group. Nearctic-Neotropical. North America: *C. discolor,* n. sp., *C. huachucae* Dury.

C. krausi group. Neotropical. *C. atromaculatus* Pic, *C. superbus* Kraus. North America: *C. krausi* Dalla Torre.

C. litteratus group. Oriental-Australian. *C. insignis* Scott, *C. litteratus* Fauvel. North America: none.

C. melliei group. Neotropical. *C. melliei* Coquerel. North America: *C. crinitus,* n. sp., *C. hirsutus* Casey, *C. rotundulus,* n. sp., *C. ursulinus* Casey.

C. nitidus group (= *Eridaulus*). Holarctic. *C. jacquemarti* Mellié, *C. lineatocribratus* Mellié, *C. nitidus* (Fabricius). North America: *C. americanus* Mannerheim?, *C. biarmatus* Mannerheim, *C. ephippiatus* Mannerheim, *C. levettei* (Casey), *C. maritimus* (Hatch), *C. megastictus,* n. sp., *C. tridentatus* Mannerheim?

C. pacificus group. Oriental-Australian. *C. agariconae* Zimmerman, *C. marquesanus* Blair, *C. pacificus* Sharp. North America: none.

C. pallidus group. Nearctic-Neotropical. *C. corticinus* Gorham, *C. pallidus* Mellié. North America: *C. tetracentrum* Gorham.

C. pilosus group. Nearctic-Neotropical. *C. pilosus* Gorham. North America: *C. cornutus* Blatchley.

C. punctulatus group. Holarctic. *C. punctulatus* Gyllenhal, *C. tomentosus* Mellié. North America: *C. horridulus* Casey, *C. hystriculus* Casey.

C. setarius group (including *Apterocis*?). Australian (Hawaii). *C. bicolor* Sharp, *C. chloroticus* Sharp, *C. setarius* Sharp, *C. tabidus* Sharp. North America: none.

C. signatus group. Australian (Hawaii). *C. kauaiensis* Perkins, *C. nigrofasciatus* Blackburn, *C. roridus* Sharp, *C. signatus* Sharp. North America: none.

C. subtilis group. Nearctic-Neotropical. North America: *C. acritus,* n. sp., *C. subtilis* Mellié.

C. taurus group (= *Macrocis*). Nearctic-Neotropical. *C. bison* (Reitter), *C. diabolicus* (Reitter), *C. grandicornis* (Pic), *C. setifer* (Gorham), *C. taurus* (Reitter), *C. testaceus* (Pic). North America: *C. cornelli,* n. sp.

C. tricornis group. Nearctic-Neotropical. *C. delicatulus* (Jacquelin du Val), *C. tricornis* (Gorham). North America: *C. miles* (Casey).

C. vitulus group. Nearctic-Neotropical. *C. bubalus* Reitter, *C. bisbidens* Gorham, *C. fasciatus* Gorham, *C. granarius* Mellié. North America: *C. congestus* Casey, *C. vitulus* Mannerheim.

Members of this genus may be distinguished from other North American Ciidae by the 10-segmented antennae, rounded or angulate to dentate protibial apex without spines at the outer angle, flat to carinate prosternum without a laminate intercoxal process, angulate or produced anterior pronotal angles, simple elytral suture, and sexual modifications almost always present on the head and/or pronotum of the male. Species of *Strigocis, Sulcacis, Malacocis,* and *Ceracis* may have 10-segmented antennae, but always have spinose protibial

apices. Species of *Strigocis* and *Orthocis* have an inflexed margin at the apex of the elytral suture, and members of the latter group never have horns or tubercles on the head or pronotum of the male. Species of *Dolichocis*, *Ennearthron*, and *Plesiocis* resemble *Cis* in several respects and have rounded or dentate protibial apices, but the antennae are always 9-segmented.

In an earlier paper (Lawrence, 1965), I treated Thomson's *Eridaulus* as a full genus, characterized by the carinate prosternum, oval body form, dual elytral punctation, and triangular plates on the head of the male. Further study led me to abandon this concept (Lawrence, 1967b: 98) and to place the included species in at least two different species groups (*Cis nitidus* group and *C. pacificus* group). *Macrocis* Gorham is another genus whose species are characterized by having 10-segmented antennae, carinate prosternum, dual elytral punctation, and two plates on the head of the male. In this case, however, the body is very short and stout, and the frontoclypeal plates are produced to form long, narrow horns. I can see little reason for maintaining a separate genus for this group, although it contains a large number of Neotropical species. The prosternal structure is not uncommon in the genus *Cis*, and the long, lateral horns on the head of the male may be found in members of the *C. compressicornis* group and the *C. melliei* group.

Key to the North American Species of *Cis*

1. Vestiture of elytra distinctly dual, consisting of 2 classes of hairs or bristles, which differ in length, thickness, color, form, or angle of inclination (Figs. 29–30) 2

— Vestiture of elytra not dual, the hairs or bristles varying slightly in length, but not falling into 2 distinct classes 8

2. Vestiture of elytra consisting of short, erect bristles, which are seriate, and very fine, inclined hairs, which are not visible under 10× magnification; head of male with 2 tubercles on vertex (Fig. 5) .... *C. cayensis* (*see* 22; p. 448)

— Both classes of hairs or bristles easily visible under 10× magnification 3

3. Body shorter and broader, EL/EW usually less than 1.50 mm; if slightly more, then male with 2 subtriangular frontoclypeal plates; lateral margins of pronotum visible for their entire lengths from above, the anterior angles produced forward 4

— Body longer and narrower, EL/EW more than 1.50 mm; male with 4 frontoclypeal teeth or tubercles; lateral margins of pronotum not visible for their entire lengths from above, the anterior angles not produced 7

4. Erect bristles only slightly longer than inclined ones; abdominal fovea in male absent or located on posterior part of sternite III 5

— Erect bristles at least 1.50 × as long as inclined bristles or hairs; abdominal fovea in male located in center of sternite III 6

5. Size smaller, TL usually less than 1.75 mm; elytral punctation subseriate; male with 2 subtriangular, frontoclypeal plates and an abdominal fovea .... *C. floridae* (*see* 36; p. 460)

— Size larger, TL usually more than 1.75 mm; elytral punctation confused; male with 4 frontoclypeal teeth and no abdominal fovea .... *C. huachucae* (*see* 36; p. 462)

6. Vestiture consisting of longer and shorter, fine, yellow bristles, which are subseriate on the elytra; EL/EW less than 1.33; fully pigmented adult black .... *C. cornutus* (p. 451)

— Vestiture consisting of longer, stiff and erect, dark bristles and shorter, inclined, pale hairs, which are uniformly distributed on elytra (Fig. 29); EL/EW more than 1.33; fully pigmented adult reddish brown .... *C. crinitus* (p. 453)

7. Body flattened, GD/EW usually less than 0.73; male with abdominal fovea .... *C. creberrimus* (*see* 31, 46; p. 452)

— Body subcylindrical, GD/EW usually more than 0.73; male without abdominal fovea .... *C. horridulus* (p. 462)

8. Elytral punctation dual, consisting of larger, shallow megapunctures and smaller, deeper micropunctures, which bear bristles or hairs 9

— Elytral punctation single, the punctures fairly uniform in size and all or most of them bearing hairs or bristles 29

9. Vestiture consisting of fine hairs 10

— Vestiture consisting of short, stout bristles 17

10. Elytral hairs longer, more than 0.20 × as long as scutellar base and visible under 10× magnification, decumbent 11

— Elytral hairs very short, less than 0.15 × as long as scutellar base and not visible under 10× magnification, erect or inclined 12

11. Pronotal punctation finer and sparser, punctures subequal to eye facets and separated by 1.0 to 1.5 diameters; body usually smaller, narrower, and bicolored, brownish with black pronotum and transverse elytral macula .... *C. ephippiatus* (p. 458)

— Pronotal punctation coarser and denser, punctures larger than eye facets and separated by 0.33 to 0.66 diameter; body usually larger, broader, and more uniformly pigmented, brownish .... *C. biarmatus* (p. 446)

12. Body more elongate, EL/EW more than 1.40; prosternum in front of coxae slightly tumid but not carinate (Figs. 11–12) 13

— Body shorter and broader, EL/EW less than 1.40; prosternum in front of coxae carinate (Fig. 13) 14

13. Elytral punctation distinctly seriate; sides of pronotum subparallel; pronotal punctation coarser and denser, the punctures usually separated by less than 0.50 diameter; head of the male with 2 widely spaced, frontoclypeal teeth .... *C. dunedinensis* (p. 457)

— Elytral punctation not seriate; sides of pronotum weakly rounded; pronotal punctation finer and sparser, the punctures usually separated by more than 0.50 diameter; head of male with 4 frontoclypeal teeth (the outer 2 sometimes obsolete) and 2 horns on the vertex (Fig. 5) .... *C. niedhauki* (p. 467)

14. Pronotal punctures about as large as elytral megapunctures and usually separated by more than 0.75 diameter; TL usually less than 1.40 mm; male with 2 distant, lateral horns on pronotal apex and a single, median, forked horn on frontoclypeal ridge (Fig. 6) .... *C. miles* (p. 467)

— Pronotal punctures, if separated by more than 0.75 diameter, much smaller than elytral megapunctures; TL usually more than 1.40 mm; pronotal apex in male simple or bituberculate and frontoclypeal ridge bearing 2 triangular plates (Fig. 39) 15

15. Outer edge of protibia irregularly notched or serrate for part of its length (Fig. 54); pronotal punctation finer and sparser, punctures smaller than eye facets and separated by more than 1 diameter; lateral edges of pronotum smooth; elytral punctation not distinctly seriate .... *C. levettei* (p. 464)

— Outer edge of protibia simple; pronotal punctation coarser and denser, punctures usually larger than eye facets and separated by less than 1 diameter; lateral edges of pronotum coarsely crenulate; elytral punctation distinctly seriate 16

16. Anterior angles of pronotum broadly rounded; pronotal punctures very dense, separated by 0.33 diameter or less, interspaces smooth; elytral megapunctures 4 × as large as micropunctures; abdominal fovea in male circular .... *C. megastictus* (p. 465)

— Anterior angles of pronotum subacute; pronotal punctures not as dense, separated by 0.50 to 0.66 diameter, interspaces granulate; elytral megapunctures less than 4 × as large as micropunctures; abdominal fovea in male longitudinally oval .... *C. maritimus* (p. 465)

17. Elytra short and broad, EL/EW less than 1.28, apices broadly rounded; elytral punctation distinctly seriate; prosternum strongly carinate; TL less than 1.75 mm; frontoclypeal ridge in male with 2 long and narrow, lateral horns (Fig. 42) .... *C. cornelli* (p. 450)

— Elytra longer and narrower, EL/EW more than 1.28, or if slightly less, apices narrowly rounded; male never with long, narrow horns; without other characters in combination 18

18. Anterior angles of pronotum distinctly produced forward and broadly rounded (Fig. 43); pronotum shorter and broader, PL/PW usually less than 0.80, the disc impressed anteriorly in male; lateral margins of pronotum broader, easily visible for their entire lengths from above; prosternum tumid but not carinate; size larger, TL usually more than 2.00 mm 19

— Anterior angles of pronotum not or barely produced forward and angulate; pronotum longer and narrower, PL/PW usually more than 0.80, the disc not impressed anteriorly in male; lateral margins of pronotum narrower or prosternum carinate; size smaller, TL usually less than 2.00 mm 20

19. Elytral punctation seriate; elytral bristles longer and narrower, more than 0.25 × as long as scutellar base and more than 3 × as long as wide; lateral edges of pronotum weakly and finely crenulate; pronotal and elytral discs fairly even .... *C. fuscipes* (p. 460)

— Elytral punctation confused; elytral bristles shorter and broader, less than 0.20 × as long as scutellar base and less than 3 × as long as wide; lateral edges of pronotum strongly and coarsely crenulate; pronotal

and elytral discs irregularly impressed .... *C. pistoria* (p. 469)

20. Prosternum distinctly carinate; elytra shorter and somewhat ovate, EL/EW usually less than 1.42; apex of pronotum in male produced and emarginate, forming a subtriangular process or two approximate tubercles 21

— Prosternum flat or slightly tumid, not carinate; elytra more elongate and parallel-sided, EL/EW usually more than 1.42; apex of pronotum in male simple 22

21. Elytral punctation obscurely dual, megapunctures barely larger than micropunctures .... *C. tridentatus* (p. 477)

— Elytral punctation distinctly dual, megapunctures 1.50 to 3.0 × as large as micropunctures .... *C. americanus* (p. 444)

22. Elytral punctation distinctly seriate 23

— Elytral punctation not distinctly seriate 27

23. Outer apical angle of protibia not produced, rounded, or obtusely angulate; lateral margins of pronotum broader, visible for their entire lengths from above; fully pigmented adults bicolored, with pronotum reddish and elytra black or red and black 24

— Outer apical angle of protibia at least slightly produced, usually forming a distinct tooth; lateral margins of pronotum narrower, not or barely visible for their entire lengths from above; fully pigmented adults uniformly brownish or black in color or with pronotum darker than elytra 25

24. Body larger and more elongate, TL usually more than 1.75 mm and EL/EW usually more than 1.45; elytral punctation finer and sparser; frontoclypeal ridge in male simple .... *C. versicolor* (p. 478)

— Body smaller and broader, TL usually less than 1.75 mm and EL/EW usually less than 1.45; elytral punctation coarser and denser; frontoclypeal ridge in male with 2 weak tubercles .... *C. subfuscus* (p. 476)

25. Elytral vestiture dual, consisting of short, stout bristles and very fine hairs, which are not visible under 10× magnification; TL usually less than 1.40 mm; head of male with 4 frontoclypeal teeth and 2 tubercles on vertex .... *C. cayensis* (*see* 2; p. 448)

— Elytral vestiture not dual; TL usually more than 1.40 mm; male without tubercles on vertex 26

26. Pronotal punctation sparser, punctures usually separated by more than 0.50 diameter, interspaces coarsely granulate and dull; elytral bristles yellowish; abdominal fovea in male about 0.20 × as long as body of sternite III .... *C. striolatus* (p. 475)

— Pronotal punctation denser, punctures usually separated by less than 0.50 diameter, interspaces finely granulate and shiny; elytral bristles colorless; abdominal fovea in male more than 0.25 × as long as body of sternite III .... *C. tristis* (p. 477)

27. Body more elongate, EL/EW more than 1.60; elytra yellowish with black maculae .... *C. krausi* (p. 463)

— Body less elongate, EL/EW less than 1.60; elytra uniformly brownish or black 28

28. Frontoclypeal ridge in male simple; abdominal fovea in male present; southwestern U. S. .... *C. acritus* (p. 443)

— Frontoclypeal ridge in male with 2 tubercles; abdominal fovea absent; eastern U. S. .... *C. subtilis* (p. 476)

29. Vestiture consisting of very short, fine hairs, which are not or barely visible under 10× magnification; outer apical angle of protibia blunt and rounded; body elongate, EL/EW more than 1.50; elytral suture with an inflexed margin near apex (Fig. 38); head and pronotum in male simple .... *Orthocis* (p. 484)

— Vestiture consisting of long hairs or short, stout bristles 30

30. Vestiture of long, fine hairs 31

— Vestiture of shorter, stout bristles 34

31. Body flattened and elongate, EL/EW more than 1.50; frontoclypeal ridge in male with 4 tubercles .... *C. creberrimus* (*see* 7, 46; p. 452)

— Body not flattened, shorter and broader, EL/EW less than 1.50; frontoclypeal ridge in male with 2 narrow, lateral horns (Fig. 41) 32

32. Prosternum in front of coxae carinate; metasternum short and broad, the length at midline less than 0.40 × the width; sides of elytra strongly rounded, the apices acute .... *C. rotundulus* (p. 471)

— Prosternum in front of coxae strongly tumid, but not carinate; metasternum more elongate, the length at midline more than 0.40 × the width; sides of elytra weakly rounded or subparallel, the apices blunt 33

33. Lateral edges of pronotum strongly crenulate; size smaller, TL usually less than 1.60 mm; fully pigmented adults usually reddish in color; abdominal fovea in male less than 0.20 × as long as body of sternite III .... *C. ursulinus* (p. 478)

— Lateral edges of pronotum not or weakly crenulate; size larger, TL usually greater than 1.60 mm; fully pigmented adults usually blackish in color; abdominal fovea in male more than 0.20 × as long as body of sternite III .... *C. hirsutus* (p. 461)

34. Lateral margins of pronotum broader, usually visible for their entire lengths from

above; anterior angles of pronotum distinctly produced and rounded 35
— Lateral edges of pronotum narrower, usually not visible for their entire lengths from above; anterior angles of pronotum not or barely produced and subacute 41
35. Vestiture indistinctly dual, the bristles differing in length and angle of inclination 36
— Vestiture single 37
36. Elytral punctation subseriate; size smaller, TL usually less than 1.75 mm; male with 2 subtriangular frontoclypeal plates; abdominal fovea present .... *C. floridae* (*see* 5; p. 460)
— Elytral punctuation confused; size larger, TL usually more than 1.75 mm; male with 4 frontoclypeal teeth; abdominal fovea absent .... *C. huachucae* (*see* 5; p. 462)
37. Prosternum in front of coxae carinate; size smaller, TL less than 2.20 mm; male with 2 pronotal horns, 4 frontoclypeal teeth, and a pubescent fovea .... *C. quadridentatus* (p. 469)
— Prosternum in front of coxae flat to strongly tumid, but not carinate; size larger, TL more than 2.20 mm, or if slightly less, male without above combination of characters 38
38. Lateral margins of pronotum without raised lip, edges strongly crenulate (Fig. 44); body more elongate, EL/EW more than 1.50; elytra with a transverse impression at anterior fourth; apex of pronotum in male weakly emarginate, but never with horns .... *C. discolor* (p. 455)
— Lateral margins of pronotum with a narrow, raised lip, edges not or barely crenulate (Fig. 43); body shorter and broader, EL/EW less than 1.50; elytra without transverse impression; apex of pronotum in male with 2 triangular horns 39
39. Pronotal punctures only slightly smaller than elytral punctures; elytral bristles longer and finer, more than 6 × as long as wide, acute at apex; frontoclypeal ridge in male with 2 triangular plates; male with abdominal fovea; elytra in female more than 1.90 × as long as pronotum .... *C. tetracentrum* (p. 476)
— Pronotal punctures much smaller than elytral punctures; elytral bristles shorter and stouter, less than 6 × as long as wide, blunt at apex; frontoclypeal ridge in male elevated and trisinuate, so that 4 teeth are formed (Fig. 3); male without abdominal fovea; elytra in female less than 1.90 × as long as pronotum 40
40. Pronotal punctation coarser and denser, the punctures usually separated by less than 0.75 diameter, interspaces smooth and shiny; antennal segment III less than 1.50 × as long as IV; body somewhat smaller, shorter and stouter, TL usually less than 2.45 mm; EL/EW usually less than 1.31, and TL/EW in female usually less than 2.06; southeastern U. S. .... *C. congestus* (p. 449)
— Pronotal punctation finer and sparser, the punctures usually separated by more than 0.75 diameter, the interspaces granulate and dull; antennal segment III more than 1.50 × as long as IV; body somewhat larger and more elongate, TL usually more than 2.45 mm, EL/EW usually more than 1.31, and TL/EW in female usually more than 2.06; California and northern Arizona .... *C. vitulus* (p. 479)
41. Body shorter and broader, EL/EW less than 1.40, or if slightly more, apex of pronotum in male with 2 triangular horns; elytral punctation confused 42
— Body more elongate, EL/EW more than 1.40, or if slightly less, elytral bristles subseriate; apex of pronotum in male simple, emarginate, or with 2 small tubercles 44
42. Base of scutellum less than 0.10 × as wide as pronotum; body somewhat shorter and broader, EL/EW usually less than 1.30; prosternum in front of coxae slightly tumid but not carinate; apex of pronotum in male simple, frontoclypeal ridge elevated and weakly trisinuate .... *C. laminatus* (p. 464)
— Base of scutellum more than 0.10 × as wide as pronotum; body somewhat more elongate, EL/EW usually more than 1.30; prosternum in front of coxae weakly carinate; apex of pronotum and frontoclypeal ridge in male each bearing 2 triangular plates or horns (Fig. 7) 43
43. Lateral edges of pronotum distinctly crenulate; pronotal punctation coarser and denser, the punctures usually separated by less than 0.75 diameter; pronotal surface granulate and dull; TL usually more than 1.40 mm .... *C. duplex* (p. 457)
— Lateral edges of pronotum not crenulate; pronotal punctation finer and sparser, the punctures usually separated by more than 0.75 diameter; pronotal surface smooth and shiny; TL usually less than 1.40 mm .... *C. castlei* (p. 447)
44. Elytral bristles shorter and broader, usually less than 2.5 × as long as wide, subseriate, blunt at apex; elytra usually bicolored, darker anteriorly than posteriorly .... *C. stereophilus* (p. 472)
— Elytral bristles longer and narrower, usually more than 2.5 × as long as wide, confused or acute at apex; elytra concolorous 45

45. Outer apical angle of protibia rounded (Fig. 47); elytral bristles varying in length, blunt, and yellowish ..... *C. festivulus* (p. 459)
— Outer apical angle of protibia produced, dentate or angulate; elytral bristles more uniform in length and acute or colorless 46
46. Body somewhat flattened, GD/EW usually less than 0.73; lateral edges of pronotum not or barely crenulate; elytral bristles subseriate and acute at apex ..... *C. creberrimus* (*see* 7, 31; p. 452)
— Body not flattened, GD/EW usually more than 0.73; lateral edges of pronotum distinctly crenulate; elytral bristles confused and blunt at apex 47
47. Elytral bristles shorter and broader, usually less than 3.5 × as long as wide; elytral punctation finer and sparser, the punctures usually less than 0.30 × as wide as scutellar base and separated by 0.50 diameter or more ..... *C. robiniophilus* (p. 470)
— Elytral bristles longer and narrower, usually more than 3.5 × as long as wide; elytral punctation coarser and denser, the punctures usually more than 0.30 × as wide as scutellar base and separated by 0.33 diameter or less 48
48. Elytral bristles colorless; apex of pronotum in male usually bituberculate; male without abdominal fovea ..... *C. hystriculus* (p. 463)
— Elytral bristles bright yellow in color; apex of pronotum in male simple; male with pubescent fovea on abdominal sternite III ..... *C. augustus* (p. 446)

Cis acritus NEW SPECIES

Holotype. ♂, ARIZONA: Rustler Park, 8 mi. W Portal, Cochise Co., Aug. 3, 1961, Lot 892 J. F. Lawrence, ex *Polyporus abietinus* on conifer [CAS]. Allotype, ♀, same data, [JFL].

Male. Length 1.67 mm. Body 2.23 × as long as broad, slightly convex. Head and pronotum reddish orange, elytra dark yellowish brown. Vestiture consisting of short, stout, blunt, colorless bristles. Vertex flattened with a slight median impression; frontoclypeal ridge simple. Antennal segment III 1.40 × as long as IV. Pronotum 0.85 × as long as broad, widest at middle; anterior edge moderately rounded, simple; sides weakly rounded, the margins narrow and distinctly crenulate, not visible for their entire lengths from above; anterior angles not produced forward, almost right; disc weakly convex, even; surface distinctly granulate, slightly shiny; punctures 0.20 × as large as scutellar base and separated by 0.25 to 0.75 diameter. Elytra 1.50 × as long as broad and 2.04 × as long as pronotum; sides subparallel, apices blunt; punctation dual and confused; megapunctures somewhat coarser and denser than those on pronotum, shallow and nude; each micropuncture bearing a stout, blunt, colorless bristle, which is about 0.33 × as long as scutellar base. Prosternum slightly tumid; intercoxal process 0.30 × as wide as a procoxal cavity, parallel-sided. Protibial apex slightly produced, outer apical angle almost right (Fig. 52). Metasternum 0.54 × as long as wide; suture 0.40 × as long as median length of sternum. Abdominal sternite III bearing a median, oval, pubescent fovea, which is almost 2.0 × as long as wide, 0.30 × as long as body of sternite, distinctly margined, and located anterad of center. Sternite VIII as in Figure 63. Aedeagus as in Figures 73 and 80.

Female. Length 1.75 mm. Body 2.33 × as long as broad. Vertex and frontoclypeal ridge as in male. Pronotum 0.85 × as long as broad; anterior edge as in male. Elytra 1.57 × as long as broad and 2.04 × as long as pronotum. Protibial apex as in male. Sternite III without pubescent fovea.

Variation. Pronotum yellowish to dark reddish brown, usually reddish orange or reddish brown. Elytra yellowish to brownish black, usually brownish. Pronotum usually lighter in color than elytra. Size and dimensions vary as follows in a mixed series of seven males and nine females from California, Arizona, and New Mexico:

TL mm: ♂ 1.55–1.80 (1.70 ± 0.031),
♀ 1.47–1.82 (1.66 ± 0.040);
TL/EW: ♂ 2.20–2.38 (2.27 ± 0.022),
♀ 2.18–2.44 (2.33 ± 0.030);
PL/PW: ♂ 0.82–0.88 (0.85 ± 0.007),
♀ 0.79–0.95 (0.88 ± 0.017);
EL/EW: ♂ 1.47–1.61 (1.53 ± 0.017),
♀ 1.48–1.67 (1.58 ± 0.021);

EL PL: ♂ 1.96–2.13 (2.05 ± 0.024), ♀ 2.00–2.14 (2.09 ± 0.017);
GD EW: ♂ 0.73–0.81 (0.76 ± 0.010), ♀ 0.73–0.81 (0.77 ± 0.009).

Paratypes. ARIZONA: 1, East Turkey Creek, 6 mi. W Portal, Cochise Co., July 24, 1963, Lot 1240 JFL (A. Raske, coll.), ex *Polyporus abietinus* [JFL]; 4, Hitchcock Hwy. Mi. 27, VI–22–1957 [MCZ, UAZ]; 2, Madera Canyon, Santa Rita Mts., Santa Cruz Co., Jan. 30, 1964, Lot 1285 JFL, ex *Polyporus abietinus* [JFL]; 1, 6 mi. SW Portal, Cochise Co., Aug. 2, 1961, Lot 879 JFL, ex *Polyporus abietinus* [JFL]; 3, Rustler Park, 8 mi. W Portal, Cochise Co., Aug. 3, 1961, Lot 892 JFL, ex *Polyporus abietinus* [JFL]; 1, Southwest Research Station, 5 mi. SW Portal, Cochise Co., Aug. 1, 1961, Lot 882 JFL, ex *Polyporus abietinus* [JFL]. CALIFORNIA: 1, 1 mi. SE Alta Sierra, Kern Co., July 5, 1962, Lot 1043 JFL, ex *Polyporus abietinus* [JFL]; 1, 3 mi. E Shaver Lake, Fresno Co., Sept. 1, 1960, Lot 685 JFL, ex *Polyporus abietinus* [JFL]. NEW MEXICO: 2, Las Vegas H[ot] S[prings], 5.8, Barber & Schwarz Coll. [USNM]; 1, same locality, 9.8, Barber & Schwarz Coll. [USNM]; 1, same locality, 3.8, Barber & Schwarz Coll. [USNM].

Distribution. Montane regions of southern California, Arizona, and New Mexico (Fig. 106).

Host fungi. Polyporus abietinus [7(1)].

Discussion. This species may be distinguished from most other North American *Cis* by the elongate body form, dual and confused elytral punctation, and vestiture of short, blunt, colorless bristles. It differs from *C. subtilis* in having a pubescent fovea on abdominal sternite III of the male and the frontoclypeal ridge simple in both sexes. The pronotum in *C. acritus* is usually more reddish in color and more coarsely punctate than in *C. subtilis.* Of those species occurring within the range of *C. acritus, C. versicolor* and *C. striolatus* have similar body form, dual elytral punctation, and short bristles; in both of these, however, the elytral punctation is distinctly seriate. *C. discolor* has similar pale, blunt bristles, but the size is usually larger, the punctation is single, the pronotal margins are broader, and the protibial apex is distinctly dentate (Fig. 56). Smaller specimens of *C. fuscipes* may be confused with *C. acritus,* but they differ in the broader body form and the produced and rounded anterior pronotal angles (Fig. 23).

The ranges of *C. acritus* and *C. subtilis* are allopatric and the two species are closely related, even sharing the unique type of aedeagus (Figs. 73 and 80). They are considered to be distinct species in this treatment mainly because of the lack of an abdominal fovea in the male of the eastern form. The two species do not appear to belong to any Palaearctic group and their closest relatives are to be sought among the diverse and little known Neotropical fauna.

Cis acritus is found in association with conifers at intermediate and high elevations in the mountains of the Southwest. It has been collected only on *Polyporus abietinus,* where it occurs with *Cis hystriculus* in California and with *C. horridulus* and *Ceracis powelli* in Arizona.

The name *acritus* is derived from the Greek *akritos,* meaning confused, disorderly, mixed (referring to the confused elytral punctation).

Cis americanus Mannerheim

Cis americanus Mannerheim, 1852: 360; Pielou and Verma, 1968: 1184 (dist., biol.). Type locality: "Insulae Sitkhae." Lectotype, ♂, Mannerheim Coll., MZUH.

Xestocis insolens Casey, 1898: 86. Type locality: "Pennsylvania." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Cis frosti Dury, 1917: 9; Brown, 1929: 153 (dist.); Frost, 1930: 41 (biol.). Type locality: "Orono, Maine." Holotype, ♂, Dury Coll., CIN (type lost). NEW SYNONYMY.

Cis serricollis Dury, 1917: 9; Weiss and West, 1921a: 61 (dist., biol.). Type locality: "Linn Co., Oregon." Syntypes, ♀♀, Dury Coll., CIN. NEW SYNONYMY.

Xestocis minor Hatch, 1962: 232. Type locality:

"Wheatland [Yamhill Co.], Ore." Holotype, ♂, Hatch Coll., UW. NEW SYNONYMY.
Xestocis oweni Hatch, 1962: 232. Type locality: "Seattle, Wash." Holotype, ♂, Hatch Coll., UW. NEW SYNONYMY.
Xestocis strigulosus Hatch, 1962: 231. Type locality: "Seattle, Wash." Holotype, ♂, Hatch Coll., UW. NEW SYNONYMY.
Cis hatchi, NEW NAME for *Xestocis nitidus* Hatch, 1962 (not *Anobium nitidum* Fabricius, 1792). NEW SYNONYMY.
Xestocis nitidus Hatch, 1962: 232. Type locality: "Wheatland [Yamhill Co.], Ore." Holotype, ♂, Hatch Coll., UW.

Distribution. Widespread across the northern part of North America from Alaska to Nova Scotia, south in California to Monterey County on the coast and Fresno County in the Sierra Nevada, in the Rocky Mountains south to northern Utah and Colorado, and in the Appalachian chain as far south as western North Carolina (Fig. 93). Marginal records: ALASKA: Kenai. BRITISH COLUMBIA: Terrace. ALBERTA: Cypress Hills. WISCONSIN: Bayfield Co. QUEBEC: Duparquet. MAINE: Orono, Washington Co. NEW BRUNSWICK: NE of Ludlow. NOVA SCOTIA: Portaupique. NORTH CAROLINA: Highlands, Macon Co. SOUTH DAKOTA: Hill City, Custer Co. COLORADO: Steamboat Springs, Routt Co. UTAH: Provo, Utah Co. NEVADA: 8 mi. SE Lamoille, Elko Co. CALIFORNIA: Huntington Lake, Fresno Co.; Big Sur, Monterey Co.

Host fungi. Polyporus adustus [7(5)]; *Polyporus betulinus* [7(4)]; *Stereum hirsutum* [6(4)]; *Fomes pinicola* [5(2)]; *Polyporus versicolor* [5(1)]; *Fomes annosus* [4(1)]; *Poria versipora* [3(2)]; *Steccherinum ochraceum* [3(2)]; *Pleurotus ostreatus* [3(1)]; *Polyporus sulphureus* [3(1)]; *Ganoderma tsugae* [3(1)]; *Polyporus abietinus* [3]; *Trametes mollis* [2(2)]; *Ganoderma applanatum* [2(1)]; *Polyporus resinosus* [1(1)]; *Polyporus hirsutus* [1(1)]; *Polyporus pargamenus* [1(1)]; *Polyporus squamosus* [1(1)]; *Polyporus tulipiferae* [1]; *Poria nigrescens* [1]; *Fomes fomentarius* [1]; *Polyporus biformis* [1]; *Phlebia merismoides* [1].

Discussion. This species is characterized by the relatively short and stout body form, strongly carinate prosternum, dual and confused or indistinctly seriate elytral punctation, and vestiture of short bristles. Several other sympatric forms resemble *C. americanus* in general body form, carinate prosternum, dual punctation, and secondary sexual characters (Fig. 39); of these, *C. levettei*, *C. megastictus*, and *C. maritimus* are clothed with very short, fine hairs, while *C. biarmatus* and *C. ephippiatus* have longer, decumbent, fine hairs. *Cis castlei* and *C. duplex* are similar in body form and vestiture, but both differ from *C. americanus* by having the prosternum only weakly carinate and the elytral punctation single. *Cis tridentatus* is very closely related to *C. americanus* and the two are often difficult to separate; in the latter the elytral punctation is more distinctly dual, the megapunctures being 1.5 to 3.0 × as large as the micropunctures.

This is an extremely variable, widespread, and polyphagous species, and it may represent a species complex. Mannerheim (1852) first described it on the basis of material from Sitka, Alaska, but the name was forgotten and Casey (1898) gave the name *Xestocis insolens* to specimens from Pennsylvania. Dury (1917) described *Cis frosti* from Maine and *C. serricollis* from Oregon; the types of both of these, as well as that of *insolens*, fall within the range of variation observed in western populations of *C. americanus*. In 1962, Hatch attempted to unravel this complex in the Pacific Northwest and described four more species, which I have synonymized above. One of these, *C. oweni*, may represent a distinct species (*see* below).

Cis americanus occurs across the northern part of the continent and is particularly common in the Pacific Northwest. Here two forms can be recognized that may prove to be different species. In the first, the surface of the pronotum and elytra are

relatively shiny, the lateral pronotal margins are usually broader, the elytral megapunctures are usually larger than the pronotal punctures, separated by 1 to 3 diameters, and almost as numerous as the micropunctures, so that the vestiture is sparser, the elytral bristles are longer, about 0.50 × as long as the scutellar base, and the size is usually smaller; this form is similar to the typical *C. americanus* occurring in the Northeast. In the second form, the pronotum and elytra are relatively dull, the lateral pronotal margins usually narrower, the elytral megapunctures smaller, separated by 2 to 5 diameters and much less numerous than micropunctures, so that the vestiture is denser, the elytral bristles are only about 0.33 × as long as the scutellar base, and the size is usually larger; this corresponds to Hatch's *oweni*. In California, the first form is found on several fungi, including *Stereum hirsutum*, *Steccherinum ochraceum*, and *Polyporus sulphureus*, while the second is found most often on *Polyporus adustus* and *Fomes pinicola*. The differences between the two forms are slight and intermediates may be found. The two have been collected at the same localities on several occasions and may represent sympatric sibling species. *Cis tridentatus* occurs in the same general area and is difficult to distinguish from the two forms described above; it is treated here as a distinct species because the differences, however slight, appear to be consistent. A thorough analysis of this group in the Pacific Northwest would require more field study.

This species and its sibling, *C. tridentatus*, are most closely related to members of the *Cis nitidus* group, from which they differ in the vestiture and in the form of the aedeagus (Fig. 75; cf. Fig. 74).

Cis angustus Hatch

Cis angustus Hatch, 1962: 230. Type locality: "Stanley, B. C." Holotype, ♀, CAS.

Distribution. Mountains of the Pacific Coast, from south-central British Columbia to the southern Sierra Nevada (Fig. 94). Marginal records: BRITISH COLUMBIA: Stanley. WASHINGTON: Paradise Park, 6000′, Mt. Rainier, Pierce Co. CALIFORNIA: 7 mi. N Mineral, 6000′, Tehama Co.; Huntington Lake, Fresno Co.

Host fungi. Fomes pinicola [2(2)]; *Fomes annosus* [1]; *Fomes officinalis* [1].

Discussion. This species is characterized by the long and narrow, somewhat cylindrical, body form; single, coarse, and confused elytral punctation; weakly dentate or angulate protibial apex (Fig. 52); and moderately long and fine, yellowish bristles. *Cis creberrimus* differs in being flattened and in having much finer and denser elytral punctation. *C. festivulus* has shorter and stouter, yellowish bristles, which are uneven in length, and a rounded protibial apex (Fig. 47). *C. robiniophilus* and *C. hystriculus* are both quite similar, but the former has shorter and stouter bristles and finer elytral punctures, while the latter has colorless bristles and no abdominal fovea in the male.

Cis angustus appears to be most closely related to *C. robiniophilus* from the eastern United States and *C. fagi* Waltl and *C. castaneus* Mellié from the Palaearctic region. The species has been collected only on the Pacific Coast, but further field work may reveal a broader distribution. It appears to be restricted to coniferous forests at higher elevations and may be considered part of the Holarctic faunal element. It has been found on three related species of *Fomes*.

Cis biarmatus Mannerheim

Cis biarmatus Mannerheim, 1852: 360. Type locality: " . . . Insulae Sitkhae." Lectotype, ♂, Mannerheim Coll., MZUH.

Xestocis biarmata (Mannerheim),—Casey, 1898: 86 (dist.); Fall, 1926: 200 (dist.); Hatch, 1962: 233, pl. 48, fig. 4, 4a (dist.).

Eridaulus biarmatus (Mannerheim),—Lawrence, 1965: 281.

Cis bicarinatus LeConte, 1867: 58. Incorrect subsequent spelling.

Distribution. Pacific Coast of North America, from southern Alaska to Marin Co., California (Fig. 102). Marginal records: ALASKA: Sitka; BRITISH COLUMBIA: Peachland; WASHINGTON: Carbon R., Mt. Rainier, Pierce Co.; OREGON: Sandy, Clackamus Co.; CALIFORNIA: 2 mi. SW Inverness, Marin Co.

Host fungi. Fomes pinicola [10(6)].

Discussion. Cis biarmatus may be distinguished by the short and stout body form, distinctly carinate prosternum, dual and confused elytral punctation, and vestiture of moderately long, decumbent hairs. *Cis americanus, C. tridentatus, C. megastictus, C. maritimus,* and *C. levettei* all differ in vestiture, having either short, fine hairs or short, stout bristles. In the closely related *C. ephippiatus,* the body is somewhat smaller and less uniformly pigmented, the pronotal punctation is finer and sparser, the elytral punctation is more distinctly dual and subseriate, and the anterior edge of the pronotum in the male is less strongly produced forward.

This species is relatively restricted in its distribution, occurring only along the Pacific Coast. Throughout its entire range it is sympatric with *C. ephippiatus,* but the range of the latter extends across the northern part of the continent to the Atlantic Coast. *Cis biarmatus* has been taken almost exclusively in *Fomes pinicola* growing on conifers in the coastal forests, while its sibling, *C. ephippiatus,* is most commonly collected in *Ganoderma applanatum* on hardwoods, at least on the Pacific Coast (*see* further discussion under *Cis ephippiatus,* p. 458). Other Ciidae usually collected in association with *C. biarmatus* are *Cis tridentatus, Dolichocis indistinctus* and *D. manitoba.*

Cis castlei (Dury), NEW COMBINATION

Xestocis castlei Dury, 1917: 17. Type locality: "Cincinnati, Ohio." Holotype, ♂, Dury Coll., CIN.

Distribution. Eastern North America, from extreme southern Ontario and Pennsylvania south to central Florida, west to Iowa, and south through eastern Mexico to Costa Rica (Fig. 97). Marginal records: ONTARIO: Tilbury, Essex Co.; PENNSYLVANIA: Chestnut Hill, Philadelphia Co.; FLORIDA: Highlands Hammock, 6 mi. W Sebring, Highlands Co.; LOUISIANA: 5 mi. S Livingston, Livingston Co.; MISSISSIPPI: 5 mi. N Ackerman, Choctaw Co.; IOWA: Maquoketa Caves State Park, Jackson Co.; SAN LUIS POTOSÍ: Huichihuayan; VERACRUZ: El Fortin; COSTA RICA: San José.

Host fungi. Polyporus adustus [9(4)]; *Polyporus pargamenus* [5]; *Polyporus hydnoides* [2]; *Stereum ostrea* [2]; *Polyporus mutabilis* [1(1)]; *Polyporus vinosus* [1(1)]; *Trametes corrugata* [1(1)]; *Ganoderma applanatum* [1]; *Lentinus crinitus* [1]; *Polyporus lignosus* [1]; *Polyporus zonalis* [1]; *Poria latemarginata* [1]; *Trametes plebeja* [1].

Discussion. This species differs from most North American *Cis* by the small size (TL usually less than 1.4 mm), short and broad body form, weakly carinate prosternum, single and confused elytral punctation, vestiture of short, stout bristles, pronotum with narrow lateral margins that are not crenulate, and uniquely curved, subtriangular, frontoclypeal plates in the male (Fig. 7). *Cis duplex* differs in being larger (TL rarely less than 1.4 mm) and in having the pronotum dull with coarser and denser punctation and smooth lateral edges. *C. laminatus* is much larger, with a relatively smaller scutellum, slightly tumid prosternum, and simple pronotal apex in the male. *Cis vitulus, C. congestus,* and *C. quadridentatus* differ in having the anterior pronotal angles distinctly produced forward, the lateral pronotal margins visible from above, and the frontoclypeal ridge quadridentate in the male; in addition, the first two species are much larger in size.

Cis castlei occurs throughout the eastern United States and extends into tropical Mexico and Central America. It does not

appear to be closely related to any other North American species. It has been found in a number of fungi, but *Polyporus adustus* may be the preferred host.

Cis cayensis NEW SPECIES

Holotype. ♂, FLORIDA: Big Pine Key, Monroe Co., June 4, 1968, Lot 2612 J. F. Lawrence, ex *Polyporus porrectus* ? [MCZ No. 31684]. Allotype, ♀, same data [MCZ].

Male. Length 1.27 mm. Body 2.12 × as long as broad, moderately convex. Head and pronotum blackish brown, elytra yellowish brown. Vestiture dual, consisting of moderately short, stout, blunt, yellowish bristles, and very short, fine, recurved, pale hairs. Vertex with deep, circular, median impression and two sharp, lateral tubercles; frontoclypeal ridge bearing two rounded tubercles on each side, the mesal two separated by 2.33 basal widths. Antennal segment III 2.00 × as long as IV. Pronotum 0.78 × as long as broad, widest at posterior third; anterior edge weakly rounded, slightly flattened at midline; sides moderately rounded, the margins narrow and distinctly crenulate, not visible for their entire lengths from above; anterior angles not produced forward, obtuse; disc moderately convex, even; surface coarsely granulate and dull; punctures shallow, shiny, 0.25 × as large as scutellar base, and separated by 0.50 to 1.25 diameters. Elytra 1.37 × as long as broad and 1.83 × as long as pronotum; sides weakly rounded, apices blunt; punctation dual and subseriate; megapunctures finer and denser than those on pronotum, sometimes confluent within a row, shallow and nude; micropunctures bearing either a fine, recurved, pale hair, which is about 0.25 × as long as scutellar base, or a stout, erect, blunt, yellowish bristle, which is 0.60 × as long as scutellar base. Prosternum moderately tumid and subcarinate; intercoxal process 0.45 × as wide as a procoxal cavity, parallel-sided. Protibia with outer apical angle expanded and rounded (Fig. 48). Metasternum 0.56 × as long as wide; suture 0.30 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.23 × as long as body of sternite, indistinctly margined, and located slightly anterad of center.

Female. Length 1.32 mm. Body 2.17 × as body of sternite, indistinctly margined, frontoclypeal ridge simple. Pronotum 0.77 × as long as broad; anterior edge moderately rounded. Elytra 1.46 × as long as broad and 2.06 × as long as pronotum. Protibia as in male. Sternite III without pubescent fovea.

Variation. Pronotum yellowish orange to black, usually blackish brown. Elytra yellowish to dark brown, usually yellowish brown. Tubercles on vertex and frontoclypeal ridge in male vary somewhat in size and shape. Size and dimensions vary as follows in a series of 25 males and 24 females from Big Pine Key, Florida (Lots 2612 and 2613):

TL mm: ♂ 1.02–1.37 (1.19 ± 0.019), ♀ 1.05–1.35 (1.19 ± 0.018);
TL/EW: ♂ 2.05–2.25 (2.17 ± 0.010), ♀ 2.12–2.29 (2.19 ± 0.009);
PL/PW: ♂ 0.75–0.85 (0.80 ± 0.005), ♀ 0.75–0.85 (0.80 ± 0.005);
EL/EW: ♂ 1.35–1.50 (1.42 ± 0.008), ♀ 1.41–1.52 (1.46 ± 0.007);
EL/PL: ♂ 1.71–2.00 (1.89 ± 0.013), ♀ 1.82–2.14 (2.01 ± 0.015);
GD/EW: ♂ 0.75–0.81 (0.77 ± 0.004), ♀ 0.75–0.84 (0.79 ± 0.005).

Total size range in material examined: 0.90–1.40 mm.

Paratypes. CUBA: 2, Buenos Aires, Trinidad Mts., VI. '39, Parsons [MCZ]. FLORIDA: Monroe Co.: 1, Big Pine Key, June 4, 1968, Lot 2611 JFL, ex *Polyporus porrectus* ? [JFL]; 29, same locality and date, Lot 2612 JFL, ex *Polyporus porrectus* ? [FMNH, JFL, MCZ, USNM]; 23, same locality and date, Lot 2613 JFL, ex *Polyporus porrectus* ? [JFL, MCZ]; 8, same locality and date, Lot 2615 JFL, ex *Polyporus hydnoides* [JFL]; 6, same locality and date, Lot 2616 JFL, ex *Polyporus*

hydnoides [JFL]; 4, Key Largo, N end, Feb. 10, 1968, Lot 2550 JFL (S. B. Peck, coll.), ex *Polyporus corrosus* [JFL]; 6, Lignum Vitae Key, May 28, 1968, Lot 2577 JFL, ex *Fomes robiniae* [JFL, MCZ]; 1, same locality and date, Lot 2580 JFL, ex *Polyporus hydnoides* [JFL]; 1, same locality, June 1, 1968, Lot 2596 JFL, ex *Stereum papyrinum* [JFL]; 3, same locality and date, Lot 2600 JFL, ex *Fomes robiniae* [JFL]; 2, same locality and date, Lot 2601 JFL, ex *Fomes robiniae* [JFL]; 1, same locality, June 5, 1968, Lot 2622 JFL, ex *Fomes robiniae* [JFL]; 2, same locality and date, Lot 2623 JFL, ex *Fomes robiniae* [JFL]; 3, Marathon, Mar. 15, 1968 (S. B. Peck, coll.), berlese sample B-111, litter and soil in scrub forest [MCZ]; 5, Pennekamp State Park, Key Largo, June 28, 1965, Lot 1525 JFL, ex *Polyporus porrectus* ? [JFL]; 13, same locality and date, Lot 1526 JFL, ex *Polyporus porrectus* ? [JFL, MCZ]; 2, same locality, May 29, 1968, Lot 2584 JFL, ex *Polyporus porrectus* ? [JFL].

Distribution. Florida Keys and Cuba.

Host fungi. Polyporus porrectus ? [6(4)]; *Fomes robiniae* [5]; *Polyporus hydnoides* [3(2)]; *Polyporus corrosus* [1(1)]; *Stereum papyrinum* [1].

Discussion. This species is unique among the North American Ciidae in the type of elytral vestiture, expanded and rounded protibial apex, and tubercles on the vertex of the male. The elytra bear short, erect, seriate bristles, alternating with very short and fine, inclined hairs, but the latter are not visible under lower magnifications, so that the vestiture may appear single. The expanded and rounded protibial apex and the male armature are both found in *Cis niedhauki*, but that species differs in being subglabrous, the vestiture consisting of only short, fine hairs. In general body form and seriate elytral bristles, *C. cayensis* resembles *C. striolatus* and *C. tristis*, but it differs from both in the smaller size, protibial apex, and head of the male.

This is a West Indian species and probably occurs throughout the Greater Antilles. It appears to prefer melanic conks, as does the closely related *Cis niedhauki.*

The name *cayensis* is derived from the Spanish *cayo,* meaning reef or small island (key).

Cis congestus Casey

Cis congesta Casey, 1898: 82. Type locality: "Louisiana." Holotype, ♀, Casey Coll., USNM.
Cis lodingi Dury, 1917: 6; Blatchley, 1923: 19 (dist.). Type locality: "Mobile, Ala." Syntypes, ♀♀, Dury Coll., CIN. NEW SYNONYMY.

Distribution. Southeastern United States, from Maryland south to northern Florida and west to southern Illinois and eastern Texas (Fig. 105). Marginal records: MARYLAND: Baltimore, Baltimore Co.; FLORIDA: Ormond, Volusia Co.; TEXAS: San Felipe, Austin Co.; ILLINOIS: Fountain Bluff, Jackson Co.

Host fungi. Polyporus hirsutus [3(2)]; *Polyporus pinisitus* [1].

Discussion. This species may be distinguished from most North American *Cis* by the very short and stout body form, single and confused elytral punctation, strongly tumid prosternum, distinctly produced anterior pronotal angles (Fig. 26), and vestiture of short bristles. In addition, the male has a trisinuate frontoclypeal ridge (Fig. 3), two stout horns on the pronotum, and no pubescent fovea on the abdomen. It differs from the closely related *C. vitulus* by having coarser and denser pronotal punctation, shiny pronotal surface, and a shorter and stouter body form. *Cis laminatus* has a similar build and a trisinuate frontoclypeal ridge in the male, but in that species the lateral pronotal margins are narrower, distinctly crenulate, and lack a raised lip. *Cis huachucae* is also similar and lacks the abdominal fovea in the male, but the vestiture is dual, consisting of longer and shorter bristles. In *Cis quadridentatus,* the prosternum is carinate, the size is smaller, and the anterior pronotal angles are not as strongly produced forward.

Cis congestus is restricted to the south-

eastern United States, while *C. vitulus* is found on the Pacific Coast. The two species belong to a group consisting primarily of Neotropical forms, such as *Cis bubalus* Reitter, *C. fasciatus* Gorham, *C. bisbidens* Gorham, *C. granarius* Mellié, and *C. grossus* Mellié. The few host records indicate that *Cis congestus,* like the other members of this group, prefers the whitish conks of *Polyporus hirsutus* and its relatives.

This species may be parthenogenetic, like *Cis fuscipes,* which is discussed below (p. 460) and in another paper (Lawrence, 1967a). Of all of the collections examined so far, only two contained males. In a series of 50 specimens from Mobile, Alabama, no males were found, 3 males were seen in a series of 29 specimens from Tennessee, and a single male turned up in a series of 20 specimens from North Carolina. A total of 4 males were found in the total sample of 136 specimens. Further collecting and laboratory rearing will be required to verify the possible existence of parthenogenesis.

Cis cornelli NEW SPECIES
Figure 42

Holotype. ♂, NORTH CAROLINA: Atlantic Beach, Carteret Co., May 19, 1966, Lot 1890 J. F. Lawrence (Carl Parsons, coll.), ex *Polyporus sector* on dead hardwood [MCZ No. 31685]. Allotype, ♀, same data [MCZ].

Male. Length 1.52 mm. Body 1.74 × as long as broad, strongly convex. Head and pronotum dark reddish brown, elytra dark yellowish brown. Vestiture of moderately short, fine, blunt, yellowish bristles. Vertex with a broad, shallow, median impression; frontoclypeal ridge bearing 2 lateral horns, which are about 4.0 × as long as wide at base, 0.86 × as long as pronotum, and separated by 1.5 basal widths, with mesal edges slightly and lateral edges strongly converging. Antennal segment III 1.70 × as long as IV. Pronotum 0.68 × as long as broad, widest at posterior third; anterior edge weakly rounded, flattened at middle; sides weakly rounded, the margins broad and very weakly crenulate, easily visible for their entire lengths from above; anterior angles distinctly produced forward, rounded; disc strongly convex, even; surface finely granulate and shiny; punctures 0.33 × as large as scutellar base and separated by 0.50 to 0.75 diameter. Elytra 1.14 × as long as broad and 1.90 × as long as pronotum; sides moderately rounded, apices blunt; punctation dual and seriate; megapunctures about as coarse as those on pronotum, very dense and almost confluent within rows, shallow and nude, micropunctures located mainly between rows, each bearing a moderately fine, blunt, yellowish bristle, which is 0.67 × as long as scutellar base. Prosternum strongly tumid and carinate; intercoxal process 0.40 × as wide as a procoxal cavity, parallel-sided. Protibia with outer apical angle produced and dentate (Fig. 50). Metasternum 0.38 × as long as wide; suture 0.35 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.27 × as long as body of sternite, indistinctly margined, and located anterad of center. Sternite VIII as in Figure 67. Aedeagus as in Figures 76 and 79.

Female. Length 1.57 mm. Body 1.80 × as long as broad. Vertex flattened; frontoclypeal ridge simple. Pronotum 0.69 × as long as broad; anterior edge strongly rounded. Elytra 1.17 × as long as broad and 1.86 × as long as pronotum. Protibia as in male. Sternite III without pubescent fovea.

Variation. Pronotum yellowish orange to blackish brown, usually reddish brown. Elytra yellowish to blackish brown, usually dark yellowish brown. Frontoclypeal horns in smaller males shorter and subtriangular, as little as 0.25 × as long as pronotum; in larger specimens the horns are longer and narrower and may be as much as 0.90 × as long as pronotum. Size and dimensions

vary as follows in a mixed series of 23 males and 25 females:

TL mm: ♂ 1.32–1.55 (1.49 ± 0.011), ♀ 1.45–1.72 (1.58 ± 0.013);
TL/EW: ♂ 1.71–1.88 (1.79 ± 0.011), ♀ 1.75–1.89 (1.80 ± 0.007);
PL/PW: ♂ 0.64–0.72 (0.68 ± 0.004), ♀ 0.64–0.71 (0.67 ± 0.003);
EL/EW: ♂ 1.12–1.25 (1.18 ± 0.008), ♀ 1.14–1.26 (1.19 ± 0.006);
EL/PL: ♂ 1.77–2.12 (1.93 ± 0.016), ♀ 1.82–2.00 (1.93 ± 0.012);
GD/EW: ♂ 0.75–0.88 (0.80 ± 0.006), ♀ 0.76–0.84 (0.80 ± 0.004).

Paratypes. FLORIDA: 5, 5 mi. W Gainesville, Alachua Co., Nov. 29, 1963, H. S. Dybas, No. 63–86 (S. B. Peck, coll.), live oak litter [FMNH, JFL]. NORTH CAROLINA: 12, Atlantic Beach, Carteret Co., May 19, 1966, Lot 1890 JFL (Carl Parsons, coll.), ex *Polyporus sector* [JFL, MCZ, USNM]; 4, Randolf Co., XII–18–63, J. F. Cornell [JFC, JFL]. SOUTH CAROLINA: 35, Yemassee, Beaufort Co., XII–28–63 (J. F. Cornell, coll.), berlese from litter under log in palmetto-cypress bog [JFC, FMNH, JFL, USNM].

Distribution. North and South Carolina and Florida.

Host fungi. Polyporus sector [1(1)].

Discussion. This species is characterized by the very short and broad body form (EL/EW less than 1.25), strongly carinate prosternum, protibial apex with a stout tooth and several spines, dual and seriate elytral punctation, vestiture of short, fine bristles, and male with a simple pronotal apex and two long and narrow, lateral horns on the clypeus. In *Cis fuscipes*, the elytra are longer and narrower, the prosternum is not carinate, and the frontoclypeal horns are absent in the male.

Cis cornelli is the only North American member of a Neotropical species group formerly included in the genus *Macrocis* (*see* p. 439). It resembles the South American species *Cis testaceus* (Pic), *C. grandicornis* (Pic), and *C. testaceimembris* (Pic), but the first two are larger (TL more than 2 mm) and the last two have broader, blunt, frontoclypeal horns in the male. *C. setifer* (Gorham), known from Mexico and Central America, is much smaller (less than 1.3 mm) with shorter and stouter, colorless bristles.

The species is probably distributed throughout the Southern Coastal Plain. It has been named after Dr. J. F. Cornell, who collected the first series.

Cis cornutus Blatchley

Cis cornutus Blatchley, 1910: 898, fig. 353. Type locality: "Grand Chain, Posey Co." [Indiana]. Holotype, ♂, Blatchley Coll., PURD.
Cis hirsuta Casey, — Weiss and West, 1920: 8 (biol., dist.). Misidentification.

Distribution. Eastern United States, from New York south to northern Florida and west to Illinois and Arkansas. Marginal records: NEW YORK: West Point, Orange Co.; FLORIDA: Jacksonville, Duval Co.; ARKANSAS: Washington Co.; ILLINOIS: Fountain Bluff, Jackson Co.

Host fungi. Polyporus versicolor [4(3)]; *Polyporus subectus* [1(1)].

Discussion. Cis cornutus may be distinguished by the dual vestiture, consisting of longer and shorter, yellowish bristles, which are seriate on the elytra, and the short and broad body form with fairly broad lateral pronotal margins. The male bears two subtriangular plates on the frontoclypeal ridge, a single, raised, rounded process on the anterior edge of the pronotum, and a small, pubescent fovea on the abdomen. The elytral bristles are much finer than those in *C. huachucae* and fall into two distinct size classes; in addition, they are yellowish and seriate. In *C. crinitus*, the longer bristles are dark in color, the vestiture is confused, and the elytra are longer and narrower. In *C. fuscipes*, the elytral bristles may be seriate, but they are relatively uniform in length and not as fine, while the elytra are more elongate and the male armature is different.

Cis cornutus is most closely related to

Cis pilosus Gorham, described from Guatemala and occurring also in Costa Rica and Mexico. In *C. pilosus* the vestiture is longer and finer, the male fovea is absent, and the aedeagus is slightly different.

Cis creberrimus Mellié

Cis creberrimus Mellié, 1848: 357, pl. 12, fig. 5; Gorham, 1883: 222 (dist.); Casey, 1898: 80 (dist.); Blatchley, 1910: 897 (dist., biol.); Weiss and West, 1921b: 169 (dist., biol.); Blackman and Stage, 1924: 85 (biol.). Type locality: "Nouvelle Orleans." Lectotype, ♀, Pic Coll. (Chevrolat Coll.), MNHN.

Cis puberulus Mellié, 1848: 358; Gorham, 1883: 222 (dist.). Type locality: "Saint-Thomas." Holotype, ♀, Marseul Coll., MNHN. NEW SYNONYMY.

Cis nubillus Gorham, 1898: 331. Type locality: "St. Vincent: south end." Holotype, ♂, BMNH. NEW SYNONYMY.

Cis nubilus Dalla Torre, 1911: 15. Incorrect subsequent spelling.

Distribution. Eastern North America, from Vermont south to Florida and west to eastern Nebraska, Kansas, and Texas; montane regions of the Southwest; throughout the West Indies; scattered localities in Mexico, Central America, and South America as far south as Santa Catarina, Brazil; Galapagos Islands (Fig. 98). Marginal records: VERMONT: Manchester, Bennington Co. FLORIDA: Paradise Key, Dade Co. NEBRASKA: Central City, Merrick Co. KANSAS: Lawrence, Douglas Co. TEXAS: Kerrville, Kerr Co.; Brownsville, Cameron Co. NEW MEXICO: Albuquerque, Bernalillo Co. ARIZONA: Hitchcock Highway, Mile 25, Santa Catalina Mts., Pima Co.; Rustler Park, 8 mi. W Portal, Cochise Co. CALIFORNIA: 4 mi. E Running Springs, San Bernardino Co.; 1.5 mi. NW Mt. Laguna, San Diego Co. BAHAMAS: Pine Ridge, Grand Bahama Is.; 2 mi. E Conch Shell Hill, Great Inagua Is. CUBA: Pinar del Rio. JAMAICA: Windsor, 10 mi. S Falmouth, Trelawny Par. GRENADA: Mount Gay Est. (leeward side). SINALOA: 22 mi. S Espinol. GUATEMALA: El Reposo, 800′; Zapote. CANAL ZONE: Barro Colorado Is. COLOMBIA: Medellin, Antioquia Prov. VENEZUELA: Yacua, Sucre Prov. BRAZIL: Nova Teutonia, Santa Catarina. GALAPAGOS IS.: 6 mi. N Academy Bay, Santa Cruz Is. This is a composite distribution in that several closely related species are probably involved (*see* discussion below).

Host fungi. Fomes sclerodermeus [6(1)]; *Polyporus adustus* [5(1)]; *Ganoderma lucidum* [4(2)]; *Ganoderma applanatum* [4]; *Polyporus hydnoides* [3(1)]; *Fomes officinalis* [2(2)]; *Poria latemarginata* [2(2)]; *Fomes pinicola* [2(1)]; *Polyporus pargamenus* [2(1)]; *Trametes corrugata* [2(1)]; *Polyporus gilvus* [2]; *Fomes annosus* [1(1)]; *Ganoderma fulvellum* [1(1)]; *Polyporus sanguineus* [1(1)]; *Poria corticola* [1(1)]; *Daedalea elegans* [1]; *Lenzites striata* [1]; *Pleurotus* sp. [1]; *Polyporus anceps* [1]; *Polyporus hirsutus* [1]; *Polyporus sulphureus* [1]; *Polyporus supinus* [1]; *Schizophyllum commune* [1]; *Trametes hispida* [1].

Discussion. The material on which the above distributional summary is based probably represents a complex of species, which are here included under the single name *Cis creberrimus,* until a more thorough analysis is possible. In North America, the species may be distinguished from other ciids by the elongate and flattened form, narrow lateral pronotal margins, dentate protibial apex, flat prosternum, fairly coarse and dense, single, subseriate, elytral punctation, and four rounded tubercles on the frontoclypeal ridge in the male.

The surface of the pronotum is subject to considerable variation. Punctation may be fine and sparse to coarse and dense, while the surface may be granulate and dull to smooth and shiny. In North America, southwestern populations have the pronotum smooth and shiny with coarse and dense punctation, while eastern populations are characterized by having a dull pronotum with finer and sparser punctation.

The vestiture is highly variable in this complex. The elytra may be clothed with relatively short and stout bristles, which are not obviously dual, longer and finer bristles, which are erect and inclined, or long, fine hairs. Long and fine hairs are characteristic of specimens from the Chiricahua Mountains of Arizona, while the short bristles occur in midwestern and eastern populations. The dual vestiture, consisting of erect and inclined, long bristles, occurs in various populations from the Southwest and Southeast. Some specimens with long, fine hairs are known from the Southeast as well.

Using these two character complexes, the North American specimens fall into four geographic segregates: 1) typical *Cis creberrimus* with fine and sparse pronotal punctation, dull surface, and fairly short elytral bristles; 2) Floridian specimens with similar pronotal surface but with dual vestiture of erect and inclined, long bristles; 3) specimens from the mountains of southern California, Arizona, and New Mexico with coarse and dense pronotal punctation, shiny surface, and dual, long vestiture; and 4) Chiricahua Mountain specimens with similar pronotal surface and long, fine hairs. A very few specimens from Ohio, Louisiana, Mississippi, and Florida fall into the last category also.

There is some intergradation between the two eastern forms, and the increase in bristle length in the East may be clinal. The dual nature of the vestiture in southeastern populations is more obvious because of the greater length of the individual elements, and the shorter bristles of "typical" *C. creberrimus* appear to be dual upon closer examination. The situation becomes much more complex if the Mexican and West Indian forms are considered. All types occur south of the United States, but material is not abundant and patterns are difficult to discern. Two different types are rarely found together, but when this does occur it would be difficult to justify lumping the forms together as one species. Both of the described species from the West Indies (*C. puberulus* from St. Thomas and *C. nubillus* from St. Vincent) are similar to populations from the southeastern United States and are the least likely to be specifically distinct.

A preliminary analysis of the male genitalia in this complex revealed a certain amount of variation in the form of the tegmen that may be correlated with differences in vestiture described above. A more detailed analysis must be postponed until more material can be examined.

Cis creberrimus is not an uncommon species in eastern North America, but it is rarely taken in large numbers. It may be found in association with various fungi but it is usually not the dominant species in a fruiting body. It is also commonly encountered under bark. The species or complex is widespread in the New World and is one of the two ciids to occur on the Galapagos Islands, the other being *Ceracis cucullatus* (Mellié), an equally ubiquitous form (*see* Lawrence, 1967b).

Cis crinitus NEW SPECIES

Holotype. ♂, FLORIDA: Lignum Vitae Key, Monroe Co., June 5, 1968, Lot 2624 J. F. Lawrence, ex *Stereum papyrinum* [MCZ No. 31686]. Allotype, ♀, same data [MCZ].

Male. Length 1.72 mm. Body 2.30 × as long as broad, moderately convex. Head and pronotum reddish brown, elytra yellowish brown. Vestiture distinctly dual, consisting of shorter, fine, recurved, yellowish hairs, and longer, stiff, erect, darker bristles (Fig. 29). Vertex flattened; frontoclypeal ridge bearing 2 lateral horns, which are about 2 × as long as wide at base, 0.16 × as long as pronotum, and separated by 3.5 basal widths, with mesal edges subparallel and lateral edges strongly converging. Antennal segment III 1.66 × as long as IV. Pronotum 0.90 × as long as broad, widest at posterior fourth; anterior edge strongly produced and emarginate, forming 2 approximate, sharp, subtriangular horns,

which are 0.14 × as long as pronotum; sides subparallel, the margins broad and weakly crenulate, easily visible for their entire lengths from above; anterior angles distinctly produced forward, subacute; disc moderately convex, even; surface smooth and shiny; punctures 0.30 × as large as scutellar base and separated by 0.25 to 0.50 diameter. Elytra 1.43 × as long as broad and 1.65 × as long as pronotum; sides subparallel, apices blunt; punctation apparently single and confused; punctures about as large as, but sparser than, those on pronotum, each puncture bearing either a fine, recurved, yellowish hair, which is about as long as scutellar base, or a stiff, erect, dark bristle, which is 1.50 × as long as scutellar base, the hairs being more abundant than the bristles. Prosternum slightly tumid; intercoxal process 0.40 × as wide as a procoxal cavity, parallel-sided. Protibia with outer apical angle strongly produced and dentate. Metasternum 0.50 × as long as wide; suture 0.33 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.36 × as long as body of sternite, distinctly margined, and located about in center.

Female. Length 1.77 mm. Body 2.15 × as long as broad. Vertex as in male; frontoclypeal ridge simple. Pronotum 0.77 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.45 × as long as broad and 2.09 × as long as pronotum. Protibial apex only slightly produced, angulate or weakly dentate. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to dark brown, usually reddish brown. Elytra yellowish to dark brown, usually yellowish brown. Frontoclypeal ridge in smaller males bearing 2 short, subtriangular processes; in larger specimens these are represented by longer, narrow horns, which may be 0.20 × as long as pronotum. Anterior edge of pronotum in smaller males barely produced and emarginate, forming 2 small tubercles; pronotal horns in larger specimens may be 0.20 × as long as pronotum. In West Indian specimens, the erect bristles are finer and lighter in color, so that the vestiture is less obviously dual. These insular specimens are almost surely conspecific with those on the mainland, but they have not been included in the paratype series. Size and dimensions vary as follows in a mixed series of 10 males and 16 females from Florida:

TL mm: ♂ 1.52–2.12 (1.81 ± 0.054), ♀ 1.67–2.32 (1.89 ± 0.037);
TL EW: ♂ 2.16–2.33 (2.26 ± 0.018), ♀ 2.10–2.26 (2.17 ± 0.010);
PL PW: ♂ 0.79–0.94 (0.88 ± 0.015), ♀ 0.74–0.82 (0.79 ± 0.006);
EL EW: ♂ 1.38–1.47 (1.43 ± 0.008), ♀ 1.39–1.53 (1.45 ± 0.010);
EL PL: ♂ 1.61–2.00 (1.72 ± 0.040), ♀ 1.91–2.21 (2.03 ± 0.023);
GD EW: ♂ 0.72–0.83 (0.77 ± 0.010), ♀ 0.74–0.80 (0.76 ± 0.004).

Paratypes. ALABAMA: 1, Mobile, 3.4 [CIN]. FLORIDA: 1, Big Pine Key, Monroe Co., June 4, 1968, Lot 2605 JFL, ex *Polyporus* sp. [JFL]; 1, same locality and date, Lot 2616 JFL, ex *Polyporus hydnoides* [JFL]; 1, Crawl Key, Monroe Co., June 6, 1968, Lot 2630 JFL, ex *Polyporus fulvocinereus* [JFL]; 1, Dunedin, 12–7–21, W. S. B.[latchley] [PURD]; 1, same locality, 1–8–26, W. S. B. [PURD]; 1, same locality, 3–20–16, W. S. B. [PURD]; 1, same locality, 3–5–20, W. S. B. [PURD]; 2, Grassy Key, Monroe Co., June 28, 1965, Lot 1522 JFL, ex *Polyporus fulvocinereus* [JFL]; 1, Indian River, IV–7–30, J. R. Barass, Florida Fruit Fly Trap Surv. [USNM]; 3, Lignum Vitae Key, Monroe Co., June 5, 1968, Lot 2624 JFL, ex *Stereum papyrinum* [FMNH, JFL]; 1, same locality, June 1, 1968, Lot 2595 JFL, ex *Polyporus fulvocinereus* [JFL]; 1, same locality and date, Lot 2596 JFL, ex *Stereum papyrinum* [JFL]; 1, same locality and date, Lot 2597 JFL, ex *Polyporus hydnoides* [JFL]; 1, Marathon, Monroe Co.; Mar. 10, 1968, Lot 2545 JFL (S. B. Peck, coll.), ex *Ganoderma zonatum*

[JFL]; 1, Punta Gorda, II–7–40, Van Dyke Collection [CAS]; 5, St. Augustine, III–5–1940, Van Dyke Collection [CAS]; 1, Tampa, 5.4, J. L. LeConte Collection [MCZ]. GEORGIA: 1, Tybee Is., VI–23, Coll. by H. A. Wenzel [CIN]. LOUISIANA: 2, Covington, 28, V, Collection H. Soltau [USNM]. NORTH CAROLINA: 1, Longbeach, VI–12–53, G. H. Nelson, Beating *Quercus virginiana* [GHN]. TEXAS: 1, Borden, 18.6 [MCZ].

Additional material. BAHAMAS: 1, 2 mi. E Conch Shell Hill, Great Inagua, Feb., 1967, Lot 2058 JFL (A. Laska, coll.), ex *Polyporus hydnoides* [JFL]. CUBA: 1, Cayamas, 29.5, E. A. Schwarz, Collector [USNM]; 1, same locality, 29.12, E. A. Schwarz [USNM]; 1, same locality, 9.3, E. A. Schwarz [USNM]; 1, same locality, 4.2, E. A. Schwarz [USNM]; 4, same locality, 10.6, E. A. Schwarz [USNM]; 1, same locality, 12.3, E. A. Schwarz [USNM]. JAMAICA: 1, Try, nr. Falmouth, VIII–9–1966, mangrove swamp, A. T. Howden [HH]. PUERTO RICO: 18, Caja de Muertos Is., Dec. 10, 1961, Lot 1660 JFL (H. Heatwole, coll.), ex *Lenzites striata* [JFL].

Distribution. Southeastern United States, from North Carolina to Florida and west to eastern Texas, the Bahamas, and the Greater Antilles (Fig. 96).

Host fungi. Polyporus hydnoides [3(1)]; *Polyporus fulvocinereus* [3(1)]; *Stereum papyrinum* [2(2)]; *Lenzites striata* [1(1)]; *Ganoderma zonatum* [1].

Discussion. Individuals of this species are easily recognized by the unique vestiture of short, recurved hairs and long, erect bristles. In most other species with dual vestiture, there are two classes of bristles, which differ mainly in length and angle of inclination (Fig. 30), but in *C. crinitus* the large bristles are much stouter and darker in color than the short hairs (Fig. 29). In *Cis cayensis* the bristles are short, pale, and seriate, while the hairs are very small and barely visible at lower magnifications. In *C. cornutus* the two types of vestiture are not as distinct (longer, erect and shorter, inclined, yellowish bristles) and are subseriate on the elytra.

Cis crinitus belongs to the *Cis hirsutus* group, but it is the only member with distinctly dual vestiture. In *Cis hirsutus*, *C. rotundulus*, and *C. ursulinus* the vestiture consists of long, recurved, fine hairs. Individuals of *C. crinitus* are usually larger than those of *C. rotundulus* or *C. ursulinus* and smaller and more elongate than those of *C. hirsutus*.

The name *crinitus* is taken directly from the Latin word meaning hairy.

Cis discolor NEW SPECIES

Holotype. ♂, ARIZONA: Rustler Park, 8 mi. W Portal, Cochise Co., Aug. 8, 1961, Lot 922 J. F. Lawrence, ex *Fomes cajanderi* on *Pinus* sp. [CAS]. Allotype, ♀, same locality and date, Lot 918 J. F. Lawrence, ex *Fomes cajanderi* on *Pinus* sp. [CAS].

Male. Length 2.45 mm. Body 2.45 × as long as broad, moderately convex. Head blackish posteriorly, reddish orange anteriorly; pronotum reddish orange, with two broad, longitudinal, black fasciae extending from the posterior edge to the anterior fifth; elytra dark brownish posterolaterally and anteriorly along the suture, reddish orange at apices, each elytron with a vague, median, reddish orange fascia that broadens posteriorly. Vestiture of short, stout, somewhat flattened, colorless bristles. Vertex with a slight median elevation; frontoclypeal ridge bearing two rounded tubercles on each side, the mesal two separated by 1.0 basal width. Antennal segment III 1.80 × as long as IV. Pronotum 0.86 × as long as broad, widest at posterior third; anterior edge strongly rounded, slightly emarginate at midline; sides weakly rounded, the margins broad and weakly crenulate, easily visible for their entire lengths from above (Fig. 44); anterior angles distinctly produced forward, rounded; disc moderately convex, broadly impressed anteriorly; surface finely granulate and shiny; punctures varying considerably in size, 0.10 to 0.25 × as large as scutellar base, and separated by

0.20 to 0.50 diameter. Elytra 1.67 × as long as broad and 2.16 × as long as pronotum; sides subparallel, apices blunt; disc with a distinct transverse impression at anterior fourth; punctation single and confused; punctures more uniform in size and somewhat smaller than the larger of the pronotal punctures, each bearing a stout, somewhat flattened, colorless bristle, which is about 0.33 × as long as scutellar base. Prosternum slightly tumid, intercoxal process 0.43 × as wide as a procoxal cavity, broadened posteriorly. Protibia with outer apical angle produced and dentate (Fig. 56). Metasternum 0.58 × as long as wide; suture 0.26 × as long as median length of sternum. Abdominal sternite III bearing a median, oval, pubescent fovea, which is 1.40 × as long as wide, 0.17 × as long as body of sternite, distinctly margined, and located anterad of center. Sternite VIII as in Figure 62. Aedeagus as in Figures 68 and 81.

Female. Length 2.70 mm. Body 2.35 × as long as broad. Vertex as in male; frontoclypeal ridge simple. Pronotum 0.85 × as long as broad; anterior edge barely emarginate at midline. Elytra 1.61 × as long as broad and 2.04 × as long as pronotum. Protibia as in male. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to reddish brown with variable brownish or blackish markings laterally, usually reddish orange with 2 broad, blackish brown, lateral fasciae. Elytra yellowish to black with variable reddish orange markings, usually reddish orange with vague, dark brownish fasciae along the suture and lateral edges. Specimens from the Chiricahua Mountains are darker in color than those from the Santa Rita Mountains, but the latter sample consists mainly of tenerals from a single lot. The Chiricahua specimens are also significantly larger in size. Male specimens vary slightly in the development of secondary sexual characters; in some males the mesal frontoclypeal tubercles are sharper than the lateral ones. Size and dimensions vary as follows in a series of seven males and four females from Rustler Park (Chiricahua Mts.), Cochise Co., Arizona (Lots 918, 922, and 1294):

TL mm: ♂ 2.45–2.85 (2.61 ± 0.052),
♀ 2.32–2.80 (2.65 ± 0.110);
TL/EW: ♂ 2.40–2.49 (2.44 ± 0.012),
♀ 2.35–2.41 (2.38 ± 0.013);
PL/PW: ♂ 0.81–0.87 (0.85 ± 0.008),
♀ 0.83–0.90 (0.86 ± 0.014);
EL/EW: ♂ 1.64–1.72 (1.66 ± 0.012),
♀ 1.61–1.67 (1.64 ± 0.012);
EL/PL: ♂ 2.08–2.30 (2.14 ± 0.029),
♀ 2.17–2.32 (2.22 ± 0.035);
GD/EW: ♂ 0.74–0.78 (0.76 ± 0.004),
♀ 0.72–0.76 (0.74 ± 0.009).

A second series of 27 males and 19 females from Madera Canyon (Santa Rita Mts.), Santa Cruz Co., Ariz. (Lot 1282) shows the following variation:

TL mm: ♂ 1.80–2.52 (2.19 ± 0.037),
♀ 1.95–2.57 (2.28 ± 0.043);
TL/EW: ♂ 2.27–2.45 (2.38 ± 0.008),
♀ 2.31–2.54 (2.44 ± 0.016);
PL/PW: ♂ 0.82–0.90 (0.87 ± 0.004),
♀ 0.80–0.89 (0.85 ± 0.005);
EL/EW: ♂ 1.50–1.66 (1.59 ± 0.007),
♀ 1.57–1.74 (1.68 ± 0.012);
EL/PL: ♂ 1.85–2.12 (2.01 ± 0.013),
♀ 2.06–2.27 (2.19 ± 0.014);
GD/EW: ♂ 0.68–0.82 (0.75 ± 0.006),
♀ 0.68–0.80 (0.76 ± 0.006).

Total size range in material examined: 1.80–2.85 mm.

Paratypes. ARIZONA: 46, Madera Canyon, Santa Rita Mts., Santa Cruz Co., Jan. 30, 1964, Lot 1282 JFL, ex *Trametes sepium* [CAS, FMNH, JFL, MCZ, UAZ, USNM]; 3, Rustler Park, 8 mi. W Portal, Cochise Co., Aug. 8, 1961, Lot 918 JFL, ex *Fomes cajanderi* [JFL]; 1, same locality and date, Lot 922 JFL, ex *Fomes cajanderi* [JFL]; 5, same locality, Apr. 9, 1964, Lot 1294 JFL (A. Raske, coll.), ex *Fomes cajanderi* [JFL].

Distribution. Montane regions of southern Arizona.

Host fungi. Fomes cajanderi [3(3)]; *Trametes sepium* [1(1)].

Discussion. Individuals of this species are characterized by the large size; elongate body form; coarse and dense punctation, which is single and confused on the elytra; vestiture of flattened, colorless bristles; broad, crenulate, lateral pronotal margins; and, elytra with a transverse impression. The two populations comprising the type series differ both in size and color pattern, but they are almost certainly conspecific. Two other specimens from the Chiricahua Mountains have been excluded from the type series although they may belong to this species. In one the TL is less than the average for the Madera Canyon series and the elytra are yellow with two distinct black spots, while in the other the size is still smaller, the elytra are uniformly brownish, and the body is more elongate than any specimen of *C. discolor* (EL/EW = 1.79). Also in this complex are specimens from northwest of Gómez Farías, Tamaulipas, Mexico, in which the elytra are maculate, and a series from Desierto de los Leones, Mexico D. F., in which the size and color are comparable to that in the Rustler Park population, but the bristles are much flatter, blunt, and wedgelike. It is obvious that further collecting will be necessary to understand this species complex.

Cis discolor is most closely related to *C. huachucae,* described from the Huachuca Mountains and known also from Texas and northern Mexico, but the latter is shorter and broader, with dual vestiture, four sharp tubercles on the frontoclypeal ridge of the male, and no abdominal fovea.

The name *discolor* is derived from the Latin word meaning variegated.

Cis dunedinensis Leng

Cis dunedinensis Leng, 1918: 207, replacement name for *Cis pusillus* Dury, 1917 (not Gorham, 1898).

Cis pusillus Dury, 1917: 10. Type locality: "Dunedin, Fla." Lectotype, ♂, Dury Coll., CIN.

Distribution. Florida and Cuba. Marginal records: FLORIDA: Dunedin, Pinellas Co.; Crescent City, Putnam Co.; Paradise Key, Dade Co.; Biscayne, Dade Co. CUBA: Cayamas.

Host fungi. Unknown.

Discussion. This species may be distinguished by the elongate form, dual and seriate elytral punctation, coarse and dense pronotal punctation, granulate and dull pronotal surface, dentate protibial apex, and vestiture of very short and fine hairs. Individuals of *Cis niedhauki* differ in having confused elytral punctation, finer and sparser pronotal punctation, expanded and rounded protibial apex, and the presence of tubercles on the vertex of the male. Specimens of various *Orthocis* may be confused with *C. dunedinensis,* but the protibial apex is narrowly rounded, the elytral suture is inflexed apically (Fig. 38), the antennae may be 9-segmented, and the frontoclypeal region is simple in the male. All other *Cis* with a vestiture of short, fine hairs have a much shorter and broader body form.

Cis dunedinensis appears to have no close affinities with other North American species, and its relatives are to be sought among the West Indian and Central American faunas.

Cis duplex Casey

Cis duplex Casey, 1898: 82. Type locality: "California." Holotype, ♂, Casey Coll., USNM.

Distribution. Mountains of the southwestern United States and Mexico, from southern California east to north-central New Mexico and south as far as Morelos and the southern tip of Baja California (Fig. 107). Marginal records: CALIFORNIA: 1.5 mi. NW Mt. Laguna, San Diego Co.; ARIZONA: Williams, Coconino Co.; NEW MEXICO: El Porvenir, San Miguel Co.; MORELOS: Cuautla; DURANGO: 37 mi. W El Salto; BAJA CALIFORNIA SUR: La Laguna, Sierra Laguna.

Host fungi. Polyporus anceps [6(5)];

Fomes officinalis [2(2)]; *Fomes pinicola* [2(2)]; *Ganoderma oregonense* [1(1)].

Discussion. This species may be distinguished by the moderately short and broad body form; single and confused elytral punctation; weakly carinate prosternum; narrow, crenulate lateral pronotal margins; coarse and dense pronotal punctation; and vestiture of short, stout bristles. The male bears two subtriangular plates on the frontoclypeal ridge and two more on the anterior edge of the pronotum. *Cis castlei* is similar in most of these characters, but is smaller in size (TL less than 1.4 mm), somewhat shorter and broader, with shinier pronotal surface, finer and sparser pronotal punctation, smooth lateral pronotal margins, and uniquely curved frontoclypeal plates in the male (Fig. 7). The species may be confused with *Plesiocis cribrum*, which is usually larger, with 9-segmented antennae and 4 teeth on the frontoclypeal ridge of the male.

Cis duplex is a distinct species that cannot be placed in any group at this time. It occurs at higher elevations in various mountain chains from southern California and New Mexico to central Mexico. It is associated with fungi on conifers and appears to prefer *Polyporus anceps*. Specimens collected at the southern tip of Baja California are from the Sierra Laguna, where *Pinus cembroides* is abundant, according to Goldman (1916). *C. duplex* has been collected with *Plesiocis cribrum* in southern California and New Mexico and appears to replace the latter in southern Arizona.

Cis ephippiatus Mannerheim

Cis ephippiatus Mannerheim, 1853: 234. Type locality: "... insula Sitkha." Types, Mannerheim Coll., MZUH ? (not located).

Cis ephippium Dalla Torre, 1911: 10. Incorrect subsequent spelling.

Xestocis moznettei Dury, 1917: 16. Type locality: "Corvallis, Oregon." Syntypes, ♂♂ ♀♀, Dury Coll., CIN. NEW SYNONYMY.

Distribution. Western North America, from southern Alaska south in California to Alameda County and the southern Sierra Nevada, and in the Rocky Mountain Region to northern Nevada and Colorado. Also known from Vermont, New Hampshire, and the Gaspé Penninsula of Quebec (Fig. 90). Marginal records: ALASKA: Sitka. BRITISH COLUMBIA: 5 mi. NE Field. WYOMING: Jenny Lake, 6800′, Grand Teton Nat. Park, Teton Co. COLORADO: 28 mi. NW Kremmling, Grand Co. NEVADA: 8 mi. SE Lamoille, Elko Co. CALIFORNIA: Huntington Lake, Fresno Co.; Berkeley, Alameda Co. NEW HAMPSHIRE: 1 mi. W Mt. Lafayette, Grafton Co. VERMONT: Big Equinox Mtn., Bennington Co. QUEBEC: Gaspé Co.

Host fungi. *Ganoderma applanatum* [10(8)]; *Fomes pinicola* [7(4)]; *Ganoderma brownii* [2(2)]; *Fomes annosus* [1]; *Polyporus betulinus* [1]; *Polyporus resinosus* [1]; *Polyporus sulphureus* [1]; *Poria versipora* [1].

Discussion. This species may be separated from most North American *Cis* by the short, stout body form, dual and confused or subseriate elytral punctation, distinctly carinate prosternum, and vestiture of moderately long, decumbent hairs. It differs from the closely related *C. biarmatus* in the finer and sparser pronotal punctation, smaller size, dark transverse macula on the elytra, and weakly produced pronotal apex in the male. *C. ephippiatus* was described by Mannerheim from Sitka, Alaska, and although the type has not been seen, it is fairly apparent from the description that it is the same species that Dury named *Xestocis moznettei* on the basis of Oregon specimens.

Like *Cis biarmatus, C. ephippiatus* is distributed along the Pacific Coast, but the latter also occurs in the Rocky Mountains and in the northeastern part of the continent (Figs. 90 and 102). Where the two species occur together, the former is found in conks of *Fomes pinicola*, while the latter is usually taken in *Ganoderma applanatum*. Outside of the range of *Cis*

biarmatus, however, *C. ephippiatus* commonly inhabits *Fomes pinicola*.

Cis festivulus NEW SPECIES

Holotype. ♂, DISTRICT OF COLUMBIA: Wash[in]gt[o]n, 15.8, Coll. Hubbard & Schwarz [USNM]. Allotype, ♀, MARYLAND: Blad[e]ns-b[ur]g, 13.7, Coll. Hubbard & Schwarz [USNM].

Male. Length 1.62 mm. Body 2.41 × as long as broad, strongly convex. Head and pronotum dark reddish brown. Elytra dark brown. Vestiture of short, stout, blunt, yellowish bristles, which vary in length. Vertex slightly convex; frontoclypeal ridge bearing 2 blunt, setiferous tubercles, which are separated by 1 basal width. Antennal segment III 1.40 × as long as IV. Pronotum 0.84 × as long as broad, widest at posterior third; anterior edge strongly rounded, simple; sides weakly rounded, the margins narrow and weakly crenulate, barely visible for their entire lengths from above; anterior angles not produced forward, almost right; disc strongly convex, even; surface finely granulate to smooth and shiny; punctures 0.22 × as large as scutellar base and separated by 0.33 to 0.50 diameter. Elytra 1.63 × as long as broad and 2.09 × as long as pronotum; sides subparallel, apices blunt; punctuation single and uniform; punctures coarser and denser than those on pronotum, each bearing a stout, blunt, yellowish bristle, which may be from 0.25 to 0.33 × as long as scutellar base. Prosternum slightly tumid; intercoxal process 0.30 × as wide as procoxal cavity, subparallel. Protibial apex narrowly rounded, with slight indication of outer tooth (Fig. 47). Metasternum 0.50 × as long as wide; suture 0.52 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.42 × as long as body of sternite, indistinctly margined, and located anterad of center. Sternite VIII as in Figure 65. Aedeagus as in Figures 72 and 84.

Female. Length 1.52 mm. Body 2.44 × as long as broad. Vertex as in male; frontoclypeal ridge simple. Pronotum 0.87 × as long as broad; anterior edge as in male. Elytra 1.64 × as long as broad and 2.05 × as long as pronotum. Protibia as in male. Sternite III without pubescent fovea.

Variation. Pronotum yellowish orange to dark brown, usually dark reddish brown. Elytra yellowish to dark brown, usually dark brown or yellowish brown. Size and dimensions vary as follows in a mixed series of three males and seven females:

TL mm: ♂ 1.50–1.62 (1.55 ± 0.047), ♀ 1.42–1.87 (1.57 ± 0.058);
TL EW: ♂ 2.41–2.50 (2.45 ± 0.032), ♀ 2.33–2.44 (2.39 ± 0.015);
PL PW: ♂ 0.83–0.86 (0.84 ± 0.011), ♀ 0.82–0.87 (0.86 ± 0.007);
EL EW: ♂ 1.63–1.70 (1.67 ± 0.025), ♀ 1.59–1.65 (1.62 ± 0.009);
EL PL: ♂ 2.09–2.21 (2.15 ± 0.043), ♀ 2.00–2.17 (2.09 ± 0.027);
GD EW: ♂ 0.79–0.81 (0.80 ± 0.007), ♀ 0.79–0.84 (0.81 ± 0.008).

Paratype. MARYLAND: 4, Blad[e]ns-b[ur]g, 13.7, Coll. Hubbard & Schwarz [JFL, USNM]; 1, same locality, 20.7, Coll. Hubbard & Schwarz [USNM]; 1, Plummers I[sland], 15.7.07, E. A. Schwarz Collector [USNM]; 2, Sparrows Pt., VII–4–36, J. W. Green [CAS, JFL]. VIRGINIA: 1, Pennington Gap, 30.6 [USNM].

Distribution. Known only from Maryland, Virginia, and the District of Columbia.

Host fungi. Unknown.

Discussion. This species may be distinguished by the long and narrow, cylindrical body form, single and confused elytral punctation, vestiture of short, stout, yellowish bristles varying somewhat in length, and protibial apex narrowly rounded with only a slight indication of an outer tooth. In *Cis stereophilus* the elytral bristles are subseriate and more uniform in length, and the outer apical angle of the protibia is distinctly produced and angulate (Fig. 53). *Cis robiniophilus* differs from *C. festivulus*

in the somewhat finer punctures and distinctly dentate protibial apex (Fig. 49). In *Cis hystriculus* and *C. angustus* the bristles are longer and finer and the protibial apex is dentate or angulate.

Cis festivulus appears to be most closely related to the Palaearctic *Cis festivus* (Panzer) and its allies *C. vestitus* Mellié and *C. pygmaeus* (Marsham).

The name *festivulus* is derived from the Latin *festivus,* meaning joyous or merry, and the Latin diminutive suffix *-ulus* (refering to the similarity to *Cis festivus* and the smaller size).

Cis floridae Dury

Cis floridae Dury, 1917: 9. Type locality: "Key West, Florida." Lectotype, ♂, Dury Coll., CIN.

Distribution. Southern Georgia, Florida, and Cuba. Marginal records: GEORGIA: Savannah, Chatham Co. FLORIDA: Crescent City, Putnam Co.; Lignum Vitae Key, Monroe Co.; Key West, Monroe Co. CUBA: Cayamas.

Host fungi. Polyporus gilvus [1]; *Stereum papyrinum* [2].

Discussion. This species is characterized by the moderately short and broad, parallel-sided body form, coarse and dense punctation that is subseriate on the elytra, slightly tumid prosternum, dentate protibial apex, pronotum with distinct side margins and projecting anterior angles, and vestiture indistinctly dual, consisting of longer and shorter pale yellow bristles. The male bears two frontoclypeal plates, two pronotal horns, and an abdominal fovea that is located at the posterior end of sternite III. *Cis huachucae* and *C. cornutus* have dual vestiture, but both are larger (TL more than 2 mm) and somewhat shorter and broader (with the sides more rounded); in the former species the male lacks an abdominal fovea, while in the latter, the fovea is much smaller and more centrally located than in *C. floridae.* In *Cis crinitus* the form is similar but the vestiture is more distinctly dual and confused. *Cis quadridentatus* and *C. castlei* are also somewhat similar in general form, but the vestiture is single (consisting of short bristles), the prosternum is carinate, the elytral punctation is confused, and the abdominal fovea in the male is relatively smaller and more centrally located; *C. castlei* is also smaller (TL less than 1.4 mm) and the male of *C. quadridentatus* bears four teeth on the frontoclypeal ridge.

This is another West Indian species that does not extend further north than Florida and southern Georgia. It is not obviously related to any other species or group. There are too few records to speculate on host preference.

Cis fuscipes Mellié

Cis fuscipes Mellié, 1848: 271; Lawrence, 1967a: 1–14 (syn., dist., biol.). See Lawrence (1967a) for complete synonymy.

Distribution. Widespread and abundant throughout most of northern and eastern North America, ranging from northern British Columbia, south to Los Angeles County on the Pacific Coast, east across Canada to Nova Scotia, and south throughout eastern and midwestern United States (east of the 100th meridian) to southern Texas and Florida. Also known from Cuba, Madeira, and Hawaii. Marginal records in North America: BRITISH COLUMBIA: Terrace; NORTHWEST TERRITORY: Fort Smith; MANITOBA: Lake Dauphin; QUEBEC: Duparquet; NOVA SCOTIA: Truro; FLORIDA: Dunedin, Pinellas Co.; TEXAS: Brownsville, Cameron Co.; CALIFORNIA: Los Angeles Co. See Lawrence (1967a) for further remarks on distribution.

Host fungi. Polyporus versicolor [91 (48)]; *Polyporus hirsutus* [14(10)]; *Lenzites betulina* [12(3)]; *Polyporus pubescens* [5(1)]; *Polyporus conchifer* [3(2)]; *Ganoderma brownii* [1(1)]; *Polyporus adustus* [1(1)]; *Polyporus squamosus* [1(1)]; *Daedalea ambigua* [1]; *Fomes fraxinophilus* [1]; *Fomes pinicolor* [1]; *Ganoderma applanatum* [1]; *Polyporus subectypus* [1].

Discussion. This species is easily distinguished from other North American forms by the dual and subseriate elytral punctation, vestiture of short, erect bristles, large and stout body form with a shortened pronotum, wide lateral pronotal margins with strongly produced anterior angles, and impressed pronotal disc in the male. Most other species with dual and seriate elytral punctation are smaller, longer, and narrower, with different sexual characters and a relatively longer pronotum. *Cis cornelli* has a very short and broad body form with carinate prosternum and two long lateral horns on the clypeus of the male. *C. cornutus* is somewhat similar to *C. fuscipes* but is shorter and broader with finer, yellowish elytral bristles that fall into two size classes.

The distribution and biology of *Cis fuscipes* have been discussed in an earlier paper (Lawrence, 1967a). This is a very widespread and common species that is usually found in the fruiting bodies of *Polyporus versicolor* and its relatives. It is most closely related to *Cis seriatopilosus* Motschulsky and its allies from Siberia and Japan. Parthenogenesis in *Cis fuscipes* is discussed in detail in the paper cited above.

Cis hirsutus Casey

Cis hirsuta Casey, 1898: 83. Type locality: "Florida (Lake Worth)." Holotype, ♂, Casey Coll., USNM.

Distribution. Florida, the Bahamas, and the Greater Antilles (Fig. 95). Marginal records: FLORIDA: Enterprise, Volusia Co.; BAHAMAS: Matthew Town, Great Inagua Is.; PUERTO RICO: Arecibo; HAITI: Port au Prince; JAMAICA: Kingston; CUBA: Baños de San Vicente, Pinar del Rio.

Host fungi. Polyporus hydnoides [11(3)]; *Fomes sclerodermeus* [5(1)]; *Ganoderma zonatum* [4(3)]; *Ganoderma* sp. [3(3)]; *Trametes corrugata* [3(2)]; *Polyporus fulvocinereus* [2(1)]; *Polyporus maximus* [2]; *Polyporus pinisitus* [2]; *Ganoderma lucidum* [1(1)]; *Polyporus pargamenus* [1(1)]; *Polyporus sector* [1(1)]; *Auricularia polytricha* [1]; *Daedalea ambigua* [1]; *Ganoderma applanatum* [1]; *Polyporus iodinus* [1]; *Polyporus rigidus* [1]; *Polyporus supinus* [1].

Discussion. This species is fairly easy to recognize because of the short, broad form and vestiture of long and fine hairs, which are recurved at the apices. The male is characterized by two narrow, lateral horns on the frontoclypeal ridge and two approximate, flattened horns (deeply emarginate median process) on the apex of the pronotum. It is similar in general form and size to *Cis cornutus*, but in that species the vestiture is dual and seriate and consists of stouter bristles that are not recurved at the apices. In *C. crinitus* the vestiture is dual and the elytra are longer and narrower. *Cis hirsutus* differs from *C. rotundulus* in the larger size, more elongate metasternum, blunt elytral apices, and strongly tumid, but not carinate, prosternum. It differs from *C. ursulinus* in being somewhat larger, darker in color, with weakly crenulate lateral pronotal margins and a relatively larger abdominal fovea in the male.

Cis hirsutus belongs to a Neotropical species group that includes *C. crinitus*, *C. rotundulus*, *C. ursulinus*, *C. melliei* Coquerel, and a number of undescribed West Indian forms. The males of all of these species have two narrow, lateral, frontoclypeal horns and a median pronotal process that is usually emarginate (Fig. 41). It is quite possible that *C. hirsutus* is synonymous with *C. hirtellus* Jacquelin du Val (1857), described from Cuba. The type of the latter, however, could not be located, and the description is not sufficient for identification.

The distribution pattern suggests that *Cis hirsutus* evolved in the Greater Antilles and spread onto the mainland in relatively recent times. In Florida, the beetle breeds in several diverse fungi, but the preferred hosts throughout the range are *Polyporus*

hydnoides, *Fomes sclerodermeus*, and *Ganoderma zonatum*.

Cis horridulus Casey

Cis horridula Casey, 1898: 81. Type locality: "Pennsylvania (Westmoreland Co.)." Holotype, ♂, Casey Coll., USNM.

Cis mormonica Casey, 1898: 81. Type locality: "Utah (southwestern)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Distribution. Northern and montane regions of North America, except Pacific Coast, ranging from south-central British Columbia to the Atlantic Coast, south in the Rocky Mountain Region as far as the Chiricahua Mountains of southern Arizona and along the Appalachian chain as far as western North Carolina (Fig. 91). Marginal records: BRITISH COLUMBIA: Trinity Valley; ONTARIO: near Kenora; MAINE: Paris, Oxford Co.; NORTH CAROLINA: Highlands, Macon Co.; NEW MEXICO: El Porvenir, San Miguel Co.; ARIZONA: Rustler Park, 2 mi. W Portal, Cochise Co.; UTAH: southwestern.

Host fungi. Polyporus pargamenus [13 (6)]; *Polyporus abietinus* [9(4)].

Discussion. This species may be distinguished by the long and narrow, subcylindrical body form; distinctly dual vestiture consisting of longer and shorter, erect and suberect, colorless bristles; dentate protibial apex; and, lack of an abdominal fovea in the male. Most other species with similar form have single vestiture, but if the bristles vary somewhat in size, they are much shorter than those of *C. horridulus*.

This is closely related to *Cis hystriculus* and to *Cis punctulatus* and its relatives in Eurasia. The Old World species most closely resembling *C. horridulus* is *C. tomentosus* Mellié, which is known from eastern Europe and the Caucasus region. *Cis horridulus* is distributed throughout most of the northern part of the continent (extending south at higher altitudes) where it breeds in the fruiting bodies of *Polyporus pargamenus* and the related *P. abietinus*. It is replaced on the Pacific Coast by *C. hystriculus* (*see* discussion on p. 463).

Cis huachucae Dury

Cis huachucae Dury, 1917: 8. Type locality: "Huachuca Mountains, Arizona. Miller Canyon." Holotype, ♂, Dury Coll., CIN.

Distribution. Southern Arizona, Texas, and northeastern Mexico. Marginal records: ARIZONA: Miller Canyon, Huachuca Mts., Cochise Co.; TEXAS: San Antonio, Bexar Co.; NUEVO LEÓN: Chipinque Mesa, Monterrey.

Host fungi. Unknown.

Discussion. Individuals of this species are relatively large (more than 2 mm), short and broad, with dual vestiture, consisting of shorter and longer, colorless bristles, pronotum with broad lateral margins and produced anterior angles, and male with two pronotal horns, four frontoclypeal teeth or tubercles, and no fovea on the abdomen. *Cis floridae* has similarly dual vestiture but is smaller and more parallel-sided, with subseriate, yellowish bristles, and with two frontoclypeal plates and an abdominal fovea in the male. In *Cis cornutus*, the elytral bristles are longer, finer, more distinctly dual, and yellowish, while the male possesses an abdominal fovea and subtriangular frontoclypeal plates. *Cis quadridentatus, C. vitulus*, and *C. congestus* are all similar with respect to general form and sexual ornaments on the head and pronotum of the male; in the first the size is smaller, the vestiture single, the prosternum carinate, and the abdomen foveate in the male, while in the last two forms the vestiture is single, the prosternum strongly tumid, and the body somewhat stouter and more convex.

Cis huachucae appears to be most closely related to *Cis discolor*, which differs in general form, being more elongate and parallel-sided, with vestiture that is not obviously dual. The frontoclypeal ridge in the male of *C. discolor* bears four rounded tubercles, an abdominal fovea is present

but small, and the aedeagus (Figs. 68 and 81) is similar to that of *C. huachucae*. Both species are part of a complex of undescribed forms from the mountains of Mexico.

Cis hystriculus Casey

Cis hystricula Casey, 1898: 82; Hatch, 1962: 250 (dist.). Type locality: "California (Lake Tahoe)." Holotype, ♂, Casey Coll., USNM.

Distribution. Western British Columbia, Washington, and Oregon, south through the Sierra Nevada and coastal California to the Transverse Ranges in the southern part of the state (Fig. 91). Marginal records: BRITISH COLUMBIA: Terrace; OREGON: Base of Mt. Pitt, Klamath Co.; CALIFORNIA: Ebbett's Pass, 8730′, Alpine Co.; 2 mi. NE Idyllwild, Riverside Co.

Host fungi. Polyporus abietinus [27(16)]; *Poria cinerascens* [1]; *Poria versipora* [1].

Discussion. This species is characterized by the long and narrow, subcylindrical body form; single, coarse and confused elytral punctation; vestiture of short, colorless bristles; distinctly dentate protibia; and, lack of an abdominal fovea in the male. The similar *C. angustus* has yellowish bristles, a blunt and angulate protibial apex, and an abdominal fovea in the male. *Cis horridulus* resembles this species, but differs in having longer elytral bristles that fall into two size classes (dual vestiture).

Cis hystriculus is most closely related to *Cis punctulatus* Gyllenhal from northern and central Europe, and the two may represent a single Holarctic species. The adults of *C. punctulatus* that I have examined are practically indistinguishable from those of the North American species and the larva illustrated by Saalas (1923) has urogomphi similar to those of *C. hystriculus* larvae. In addition, both species breed in the same fungi (*Polyporus abietinus*). The situation becomes more complicated, however, if one considers the other species in the complex, such as *Cis horridulus* in North America, *C. tomentosus* in Europe and probably several more species from Europe and Asia.

Cis hystriculus is restricted to the Pacific Coast. It appears to be distinct from *C. horridulus* throughout most of its range, but a population from Riverside County, California (San Jacinto Mountains), exhibits slightly longer bristles and a more convex body form, approaching the condition of *C. horridulus* specimens from the mountains of southern Arizona. In southern British Columbia, however, the two species occur within 120 miles of one another and remain quite distinct. Larvae and male genitalia of the two are similar and the host fungi are the same, so that it is quite possible that they represent geographic races. If so, a zone of intergradation may be found in British Columbia in the vicinity of the Lillooet and Fraser Rivers.

Cis krausi Dalla Torre

Cis krausi Dalla Torre, 1911: 13; Blatchley, 1928: 68 (dist.). Replacement name for *Cis bimaculatus* Kraus, 1908 (not Sharp, *in* Blackburn and Sharp, 1885; not Germain, 1855).

Cis bimaculatus Kraus, 1908: 76. Type locality: "Victoria, Tex." Holotype, ♀, USNM.

Cis duryi Leng, 1918: 207. Replacement name for *Cis bicolor* Dury, 1917 (not Sharp, 1879). NEW SYNONYMY.

Cis bicolor Dury, 1917: 7. Type locality: "Tybee Island, Ga." Lectotype, ♂, Dury Coll., CIN.

Distribution. Georgia, Florida, and southern Texas. Marginal records: GEORGIA: Tybee Is., Chatham Co. FLORIDA: Dunedin, Pinellas Co.; Coconut Grove (Biscayne), Dade Co.; Key West, Monroe Co. TEXAS: Columbus, Colorado Co.; Victoria, Victoria Co.; Brownsville, Cameron Co.

Host fungi. Unknown.

Discussion. This species is fairly easily distinguished by the very long and narrow body form (EL/EW greater than 1.60), dual and subseriate elytral punctation, pronotum with narrow lateral margins and coarse, dense punctures, yellowish color with black markings, and vestiture of short, colorless bristles. The male bears two setiferous tubercles on the clypeus and an abdominal fovea that is located at the

anterior end of sternite III. Among North American species, *Cis stereophilus* is similar in several respects, but in that species the form is not as elongate, the punctation is not dual, and the elytra, although bicolored, are not maculate. The coloration in *C. krausi* is usually as follows: pronotum yellow with a large blackish patch anterad of center; elytra yellow with an anterior black triangle and two round, posterior, black spots.

This species apparently belongs to a group of West Indian forms, including *Cis superbus* Kraus (Cuba), *C. atromaculatus* Pic (Guadeloupe), and several undescribed. *C. superbus* is smaller than *C. krausi* with coarser and denser pronotal punctation, more prominent frontoclypeal tubercles, and a more centrally located abdominal fovea in the male. *C. atromaculatus* differs mainly in color pattern.

Cis krausi has been collected beneath the bark of a grapefruit tree and has been beaten from oak limbs in Florida.

Cis laminatus Mellié

Cis laminatus Mellié, 1848: 318, pl. 11, fig. 16. Type locality: "Montrieux, près de Toulon" [France]. Lectotype, ♂, Marseul Coll., MNHN.

Distribution. In North America, known only from Albany, New York. In Europe, recorded from France, Italy, Germany, Poland, Czechoslovakia, and Hungary.

Host fungi. Recorded from *Polyporus volvatus.* In Europe the species has been collected in fungi growing on pine and spruce.

Discussion. This species may be distinguished by the short and broad body form; coarse and dense punctation, which is single and confused on the elytra; vestiture of short bristles; relatively small scutellum; slightly tumid prosternum; and, the simple pronotal apex and well-developed, trisinuate, clypeal plate in the male. *Cis vitulus* and *C. congestus* are similar, but both have broader lateral pronotal margins with produced anterior angles, strongly tumid prosternum, and two pronotal horns and no abdominal fovea in the male. *Plesiocis cribrum* resembles this species and also feeds on *Polyporus volvatus,* but the antennae in *P. cribrum* are 9-segmented and the clypeus of the male bears four sharp teeth.

Cis laminatus has been collected only once at Albany, New York, in 1920. It was probably introduced from Europe and may not be established in this country. The species appears to be most closely related to *Cis fissicornis* Mellié, which occurs throughout northern Eurasia.

Cis levettei (Casey), NEW COMBINATION

Xestocis levettei Casey, 1898: 85; Dury, 1917: 17 (dist.); Gibson, 1918: 113 (dist.); Weiss and West, 1920: 8 (dist., biol.); Hatch, 1924: 305 (dist., biol.); Peterson, 1957: 94–95, fig. C5–F, 192–193, fig. C54–G (larva); Hatch, 1962: 233 (dist.). Type locality: "... Indiana ..."? Holotype, ♂, Casey Coll., USNM.

Xestocis levellei Dalla Torre, 1911: 20. Incorrect subsequent spelling.

Eridaulus levettei (Casey),—Lawrence, 1965: 281; Pielou and Matthewman, 1966: 1310 (dist., biol.); Pielou and Verma, 1968: 1184 (dist., biol.).

Distribution. Widespread in North America east of the 100th meridian, from Newfoundland south to Alabama and west to Manitoba, Kansas, and Texas. In the western part of the continent, recorded from Alberta, northwestern Colorado, eastern British Columbia and Washington, and California (Fig. 88). Marginal records: WASHINGTON: Palouse, Whitman Co.; BRITISH COLUMBIA: Trinity Valley; ALBERTA: Edmonton; MANITOBA: Aweme; NEWFOUNDLAND: Bay of Islands; SOUTH CAROLINA: Yemassee, Beaufort Co.; ALABAMA: Mobile, Mobile Co.; KANSAS: Salina, Saline Co.; COLORADO: Steamboat Springs, Routt Co.; CALIFORNIA: (no specific locality). The California specimens, if they are not mislabeled, were probably collected in the northern part of the state or in the Sierra Nevada.

Host fungi. Ganoderma applanatum [67(36)]; *Fomes fomentarius* [17(11)];

Fomes pinicola [16(13)]; *Ganoderma tsugae* [9(4)]; *Fomes connatus* [4(3)]; *Polyporus versicolor* [3]; *Ganoderma lucidum* [2(1)]; *Polyporus betulinus* [2(1)]; *Polyporus pargamenus* [2]; *Polyporus pubescens* [2]; *Stereum ostrea* [2]; *Daedalea confragosa* [1(1)]; *Polyporus resinosus* [1(1)]; *Poria nigrescens* [1(1)]; *Fomes robiniae* [1]; *Lenzites betulina* [1]; *Polyporus adustus* [1]; *Polyporus squamosus* [1]; *Poria vitrea* [1].

Discussion. This species differs from most North American *Cis* by the short and broad body form, distinctly carinate prosternum, dual and confused elytral punctation, vestiture of very short, fine hairs, and by the protibia (Fig. 54), which is irregularly serrate along the outer edge and bears a stout tooth at the apex. *Cis maritimus* and *C. megastictus* are similar in most of the above characters, but the outer edge of the protibia is simple, the pronotal punctation is coarser and denser, the lateral edges of the pronotum are crenulate, and the elytral punctation is seriate.

Cis levettei belongs to the *Cis nitidus* group, which has recently received some attention by European workers (Lohse, 1964; Strand, 1965) and includes the following Palaearctic species: *C. glabratus* Mellié, *C. hanseni* Strand, *C. jacquemarti* Mellié, *C. lineatocribratus* Mellié, and *C. nitidus* (Fabricius). The serrations on the outer edge of the protibia are definitely present in *C. glabratus* and are weakly indicated in *C. jacquemarti.*

This species is fairly common throughout the eastern part of the continent but has been collected only a few times in the Northwest. It breeds in several fungi but appears to prefer *Ganoderma applanatum* and is often found in association with *Ceracis sallei* and the tenebrionid beetle *Bolitotherus cornutus* (Panzer) (Heatwole, 1968; Lawrence, 1967b; and Pace, 1967).

Cis maritimus (Hatch), NEW COMBINATION

Xestocis martimus Hatch, 1962: 233. Type locality: "Ocean Park, Ore." Holotype, ♂, Hatch Coll., UW.

Distribution. Pacific Coast from extreme northwestern California to southwestern British Columbia. Also known from south-central Manitoba (Fig. 88). Marginal records: BRITISH COLUMBIA: Bowser; MANITOBA: Dauphin; OREGON: Blue River, Lane Co.; CALIFORNIA: Crescent City, Del Norte Co.

Host fungi. Polyporus schweinitzii [2(1)]; *Fomes pini* [1(1)].

Discussion. Cis maritimus differs from most other North American *Cis* in the short and broad body form, distinctly carinate prosternum, protibial apex with an outer tooth, dual elytral punctation, and subtriangular frontoclypeal plates in the male. It may be distinguished from related species in the *Cis nitidus* group (*see* p. 438) by the vestiture of very short, fine hairs, the finely granulate and shiny pronotum, which is coarsely and densely punctate, the produced and acute anterior pronotal angles, and the longitudinally oval abdominal fovea in the male. It is most similar to *C. levettei* of eastern North America, but that species has much finer and sparser pronotal punctation, duller pronotal surface, and serrate outer protibial edge.

Except for the single Manitoba record, the species is known only from the narrow coastal strip extending from northwestern California to southern British Columbia. It has been found in two species of fungi having reddish brown fruiting bodies. In all of North America, this is the only ciid species with a northern distribution that breeds in this type of sporophore; other Ciidae inhabiting these fungi are southern species with Neotropical affinities.

Cis megastictus NEW SPECIES
Figure 39

Holotype. ♂, CALIFORNIA: Bucks Lake, Plumas Co., July 26, 1964, Lot 1307 J. F. Lawrence (J. Doyen, coll.), ex *Fomes*

annosus on *Abies concolor* [CAS]. Allotype, ♀, same data [CAS].

Male. Length 1.70 mm. Body 1.94 × as long as broad, strongly convex. Head and pronotum reddish brown, elytra yellowish brown. Vestiture of very short and fine yellowish hairs. Vertex with a slight median impression; frontoclypeal ridge bearing two broad, subtriangular plates, which are separated by 0.80 basal width. Antennal segment III 1.60 × as long as IV. Pronotum 0.75 × as long as broad, widest at posterior two-fifths; anterior edge strongly rounded, barely flattened at middle; sides weakly rounded, the margins broad and weakly crenulate, easily visible for their entire lengths from above; anterior angles distinctly produced forward, rounded; disc strongly convex, with a narrow, median furrow extending from posterior edge to anterior fifth; surface smooth and shiny; punctures 0.25 × as large as scutellar base and separated by 0.20 to 0.25 diameter. Elytra 1.26 × as long as broad and 1.83 × as long as pronotum; sides moderately rounded, apices subacute; punctation dual and seriate; megapunctures much coarser than those on pronotum, very dense and almost confluent within rows, shallow and nude; micropunctures located within and between rows, each bearing a fine, yellowish hair, which is about 0.17 × as long as scutellar base. Prosternum strongly tumid and carinate; intercoxal process 0.38 × as wide as a procoxal cavity, narrowing posteriorly. Protibia with outer apical angle produced and dentate (Fig. 55). Metasternum 0.50 × as long as wide; suture 0.28 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.43 × as long as body of sternite, indistinctly margined, and located about in center. Sternite VIII as in Figure 64. Aedeagus as in Figures 74 and 78.

Female. Length 1.92 mm. Body 2.03 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.77 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.32 × as long as broad and 1.85 × as long as pronotum. Protibia as in male. Sternite III without pubescent fovea.

Variation. Pronotum yellowish orange to dark reddish brown, usually reddish brown. Elytra yellowish to dark brownish, usually yellowish brown. Frontoclypeal plates in smaller males shorter and more rounded. Size and dimensions vary as follows in a mixed series of six males and thirteen females from California:

TL mm: ♂ 1.70–2.07 (1.80 ± 0.057), ♀ 1.72–2.10 (1.94 ± 0.030);
TL EW: ♂ 1.89–2.06 (1.96 ± 0.028), ♀ 1.97–2.03 (2.00 ± 0.006);
PL PW: ♂ 0.71–0.81 (0.76 ± 0.014), ♀ 0.76–0.84 (0.80 ± 0.007);
EL EW: ♂ 1.24–1.36 (1.30 ± 0.018), ♀ 1.26–1.37 (1.29 ± 0.011);
EL PL: ♂ 1.76–1.92 (1.83 ± 0.021), ♀ 1.69–1.89 (1.78 ± 0.018);
GD EW: ♂ 0.78–0.82 (0.79 ± 0.007), ♀ 0.79–0.83 (0.81 ± 0.004).

Paratypes. CALIFORNIA: 4, (no specific locality) [MCZ]; 8, Bucks Lake, Plumas Co., July 26, 1964, Lot 1307 JFL (J. Doyen, coll.), ex *Fomes annosus* on *Abies concolor* [CAS, JFL, USNM]; 1, same locality and date, Lot 1305 JFL (J. Doyen, coll.), ex *Polyporus sulphureus* [JFL]; 4, Calaveras [CIN]; 1, Plaskett Meadows, 6200′, Glenn Co., July 3, 1960, Lot 631 JFL, ex *Fomes pinicolor* [JFL].

Distribution. Known only from montane regions in northern California.

Host fungi. *Fomes annosus* [1(1)]; *Fomes pinicola* [1]; *Polyporus sulphureus* [1].

Discussion. This species is distinguished by the short and broad body form, carinate prosternum, distinctly dual and seriate elytral punctation, vestiture of short, yellowish hairs, broad lateral pronotal margins with produced and rounded anterior angles, coarse and dense pronotal punctation, and dentate protibial apex. *Cis cornelli, C.*

americanus, and *C. tridentatus* all differ in the vestiture of short, stout bristles. In *C. levettei*, the pronotal punctation is much finer and sparser, the lateral pronotal margins are narrower, and the outer edge of the protibia is serrate (Fig. 54). In *C. maritimus*, the anterior pronotal angles are acute, the elytral megapunctures are not as large, and the abdominal fovea in the male is oval, rather than circular.

This is another of the localized Pacific species in the *Cis nitidus* group (the others being *C. tridentatus, C. biarmatus*, and *C. maritimus*). It occurs at higher elevations in the conifer forests of northern California but is apparently absent from the immediate coast.

The name *megastictus* is derived from the Greek *megas*, meaning large, and the Greek *stiktos*, meaning punctured (referring to the size of the elytral megapunctures).

Cis miles (Casey), NEW COMBINATION

Xestocis miles Casey, 1898: 85; Blatchley, 1928: 68 (dist., biol.); Lawrence, 1967b: 98. Type locality: "Pennsylvania (Westmoreland Co.)." [St. Vincent]. Holotype, ♂, Casey Coll., USNM.

Distribution. Eastern North America, from New York south to central Florida and west to Arkansas and Louisiana. Marginal records: NEW YORK: Pompey, Onondaga Co.; FLORIDA: Highlands Hammock State Park, Highlands Co.; LOUISIANA: (no specific locality); ARKANSAS: Washington Co.

Host fungi. Polyporus versicolor [7(1)]; *Lenzites betulina* [3(2)]; *Polyporus subectypus* [1(1)]; *Polyporus supinus* [1]; *Stereum ostrea* [1].

Discussion. This species is characterized by the small size (TL usually less than 1.4 mm), short and broad body form, carinate prosternum, very fine and sparse punctation, vestiture of very short and fine hairs, and unique male armature consisting of two lateral horns on the pronotal apex and a single, median, forked horn on the frontoclypeal ridge (Fig. 6). *Cis levettei* and *C. maritimus* are both larger, with coarser and denser elytral punctation and different sexual characters.

Cis miles is the only North American member of a Neotropical species group which includes *C. tricornis* Gorham, *C. delicatulus* (Jacquelin du Val), and a number of undescribed forms. This species, like most other members of the group, feeds primarily on *Polyporus versicolor* and its relatives.

Cis niedhauki NEW SPECIES

Holotype. ♂, FLORIDA: Lignum Vitae Key, Monroe Co., May 28, 1968, Lot 2577 J. F. Lawrence, ex *Fomes robiniae* [MCZ No. 31690]. Allotype, ♀, same data [MCZ].

Male. Length 1.30 mm. Body 2.17 × as long as broad, moderately convex. Head reddish brown, pronotum and elytra blackish. Vestiture of very short and fine, pale hairs. Vertex with a deep circular median impression, a sharp conical posteromedian tubercle, and two diverging, anterolateral blunt horns, which are about 2.0 × as long as wide at base, 0.22 × as long as pronotum and separated by 3.5 basal widths; frontoclypeal ridge bearing two tubercles on each side, the lateral two smaller and rounded, the mesal two larger, conical, and separated by 3.0 basal widths (Fig. 5). Antennal segment III 1.70 × as long as IV. Pronotum 0.78 × as long as broad, widest at anterior two-fifths; anterior edge produced and emarginate, forming two small approximate tubercles; sides moderately rounded, the margins narrow and weakly crenulate, not visible for their entire lengths from above; anterior angles not produced forward, almost right; disc moderately convex, slightly impressed anteriorly; surface granulate and slightly shiny; punctures 0.20 × as large as scutellar base and separated by 0.75 to 1.25 diameters. Elytra 1.42 × as long as broad and 1.89 × as long as pronotum; sides weakly rounded, apices blunt; punctation dual and confused; megapunctures coarser and denser than those on pronotum; each micropuncture bearing a very fine,

erect pale hair, which is about 0.10 × as long as scutellar base. Prosternum moderately tumid and subcarinate; intercoxal process 0.37 × as wide as a procoxal cavity, narrowed posteriorly. Protibia with outer apical angle expanded and rounded. Metasternum 0.58 × as long as wide; suture 0.23 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea which is 0.25 × as long as body of sternite, indistinctly margined, and located slightly anterad of center.

Female. Length 1.15 mm. Body 2.09 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.79 × as long as broad; anterior edge moderately rounded. Elytra 1.41 × as long as broad and 2.07 × as long as pronotum. Protibia as in male. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to black, usually dark reddish brown or black. Elytra yellowish to black, usually black, occasionally somewhat reddish posteriorly. Median tubercle of vertex and frontoclypeal tubercles in smaller males obscure or absent and lateral horns short and rounded; in larger males the lateral horns are strongly diverging and may be 0.25 × as long as pronotum. Size and dimensions vary as follows in a series of 25 males and 22 females from Lignum Vitae Key, Monroe Co., Florida (Lots 2547, 2577, 2601, 2622):

TL mm: ♂ 1.00–1.35 (1.15 ± 0.016), ♀ 0.97–1.32 (1.18 ± 0.018);
TL/EW: ♂ 2.09–2.26 (2.17 ± 0.010), ♀ 2.04–2.30 (2.15 ± 0.013);
PL/PW: ♂ 0.75–0.83 (0.79 ± 0.004), ♀ 0.76–0.87 (0.80 ± 0.005);
EL/EW: ♂ 1.35–1.53 (1.42 ± 0.008), ♀ 1.35–1.53 (1.43 ± 0.009);
EL/PL: ♂ 1.81–2.08 (1.90 ± 0.014), ♀ 1.88–2.13 (2.00 ± 0.015);
GD/EW: ♂ 0.71–0.81 (0.77 ± 0.004), ♀ 0.73–0.83 (0.77 ± 0.006).

Paratypes. FLORIDA: 3, Lignum Vitae Key, Monroe Co., Mar. 15, 1968, Lot 2547 JFL (S. B. Peck, coll.), ex *Fomes robiniae* [MCZ]; 19, same locality, May 28, 1968, Lot 2577 JFL, ex *Fomes robiniae* [FMNH, JFL, USNM]; 14, same locality, June 1, 1968, Lot 2601 JFL, ex *Fomes robiniae* [JFL, MCZ]; 9, same locality, June 5, 1968, Lot 2622 JFL, ex *Fomes robiniae* [JFL, MCZ].

Distribution. Known only from Lignum Vitae Key, Florida.

Host fungi. Fomes robiniae [4(2)].

Discussion. This species, like *C. cayensis*, is unique in having the protibial apex expanded and rounded (but not spinose), and the head of the male bearing armature on the vertex as well as on the frontoclypeal ridge. *Cis cayensis* males lack the median tubercle and the lateral tubercles on the vertex are not as long; in addition the vestiture is entirely different. The elongate body form, dual elytral punctation, and vestiture of short, fine hairs distinguish this species from all North American *Cis*, with the exception of *C. dunedinensis*, in which the elytral punctation is seriate, the pronotum more parallel-sided with coarser and denser punctation, and the head of the male with two frontoclypeal teeth only. Smaller specimens of *Orthocis* species may resemble *C. niedhauki*, but they will usually differ in the narrowly rounded protibial apex (Fig. 45), the nature of the elytral apices (Fig. 38), the lack of head ornaments in the male, and often in the smaller size, maculate elytra, and 9-segmented antennae.

Cis niedhauki is most closely related to *C. cayensis*, also known from the Florida Keys. It has been collected only on Lignum Vitae Key but probably occurs in the Greater Antilles. A single specimen from Cayamas, Cuba, may belong to this species, but the pronotum is somewhat shinier with coarser and denser punctation, and the color is reddish. Further specimens must be examined. *Fomes robiniae* is the only known host, but the species may occur on other melanic conks.

The species has been named in honor of

Russell and Charlotte Niedhauk, caretakers of Lignum Vitae Key, to whom I am thankful for their generous hospitality.

Cis pistoria Casey

Cis pistoria Casey, 1898: 79; Gibson, 1915: 137 (dist.); Hatch, 1924: 305 (dist.). Type locality: "Rhode Island (Boston Neck)." Holotype, ♂, Casey Coll., USNM.

Distribution. Northeastern North America from central Alberta to southern Minnesota and southern New England (Fig. 104). Marginal records: ALBERTA: Lake George, near Busby; NORTHWEST TERRITORY: Fort Smith; MANITOBA: Dauphin Lake; QUEBEC: Duparquet; MAINE: Weld, Franklin Co.; RHODE ISLAND: Boston Neck, Newport Co.; MINNESOTA: Cedar Creek Forest, Anoka Co.

Host fungi. Polyporus versicolor [7(4)]; *Polyporus pubescens* [2(2)]; *Polyporus adustus* [1(1)]; *Polyporus hirsutus* [1(1)].

Discussion. Individuals of this species are relatively large (usually more than 2.2 mm) with dual and confused elytral punctation, very short, scalelike bristles and slightly tumid prosternum. Most forms with dual punctation are narrower and more elongate and do not have the broad lateral pronotal margins and somewhat uneven pronotal disc characteristic of this species. In *Cis americanus* and *C. tridentatus*, the size is smaller, the form more oval, the prosternum carinate, and the bristles longer. *Cis fuscipes* and *C. tetracentrum* are comparable in size and general form, but in the former the elytral punctation is subseriate, in the latter it is not dual, and in both the vestiture is longer.

Cis pistoria is the only New World member of a Palaearctic group, which includes *Cis boleti* (Scopoli), *C. rugulosus* Mellié, *C. micans* (Fabricius), *C. hispidus* Gyllenhal, and *C. villosulus* (Marsham). Like most of its Old World relatives, the North American species occurs primarily on *Polyporus versicolor* and its relatives. In the Northeast it is usually found in association with *Cis fuscipes* and *Octotemnus laevis*.

Cis quadridentatus (Dury), NEW COMBINATION

Xestocis quadridentatus Dury, 1917: 17. Type locality: "Framingham, Mass." Syntypes, Dury Coll., CIN.

Cis blatchleyi Dury, 1917: 7. Type locality: "Dunedin, Fla." Lectotype, ♀, Blatchley Coll., PURD. NEW SYNONYMY.

Distribution. Eastern North America from Vermont to Florida and west as far as south-central Texas. Marginal records: VERMONT: Pawlet, Rutland Co.; FLORIDA: Dunedin, Pinellas Co.; TEXAS: San Antonio, Bexar Co.; ILLINOIS: Sayer Bog, Volo, Lake Co.

Host fungi. Unknown.

Discussion. This species may be distinguished by the short and broad body form; carinate prosternum; shiny surface; coarse and dense punctation, which is single and confused on the elytra; vestiture of short bristles; moderately broad, crenulate, lateral pronotal margins; and, male with two pronotal horns, four frontoclypeal teeth, and an abdominal fovea. *Cis vitulus* and *C. congestus* are larger in size (TL usually more than 2.2 mm) with a raised lip on the lateral pronotal margins, the prosternum not carinate, and the male without an abdominal fovea. In *C. castlei* and *C. duplex*, the lateral pronotal margins are narrower, without produced anterior angles, and the clypeus of the male bears two subtriangular plates. *Plesiocis cribrum* is similar with respect to general form, vestiture, punctation, and male armature, but in that species the antennae are 9-segmented and the pronotal margins are much narrower.

This species does not appear to be closely related to any other New World species that I have studied, but it closely resembles *Cis indicus* Pic, *Cis subsquamosus* Scott, and several undescribed forms from the Oriental Region.

Cis quadridentatus has been collected from fungus fruiting bodies and has been

found under bark on several occasions, but it has not yet been associated with a particular fungus species.

Cis robiniophilus NEW SPECIES

Holotype. ♂, OHIO: Preston, Hamilton Co., Lot 1960 JFL (A. P. Morgan, coll.), ex *Polyporus robiniophilus* (herbarium specimen, C. G. Lloyd No. 41039) [USNM]. Allotype, ♀, same data [USNM].

Male. 1.70 mm. Body 2.43 × as long as broad, moderately convex. Head and pronotum reddish brown, elytra yellowish brown. Vestiture of short, stout, blunt, yellowish bristles. Vertex slightly concave; frontoclypeal ridge bearing two blunt setiferous tubercles that are separated by 2.5 basal widths. Antennal segment III 1.50 × as long as IV. Pronotum 0.88 × as long as broad, widest at middle; anterior edge strongly rounded, simple; sides strongly rounded, the margins narrow and distinctly crenulate, not visible for their entire lengths from above; anterior angles not produced forward, almost right; disc moderately convex, even; surface finely granulate and somewhat shiny; punctures 0.17 × as large as scutellar base and separated by 0.50 to 0.75 diameter. Elytra 1.61 × as long as broad and 1.96 × as long as pronotum; sides subparallel, apices blunt; punctation single and uniform; punctures slightly coarser and denser than those on pronotum, each bearing a stout, blunt, yellowish bristle, which is about 0.33 × as long as scutellar base. Prosternum slightly tumid; intercoxal process 0.30 × as wide as a procoxal cavity, parallel-sided. Protibia with outer apical angle strongly produced and dentate (Fig. 49). Metasternum 0.60 × as long as wide; suture 0.39 × as long as median length of sternum. Abdominal sternite III bearing a median, oval, pubescent fovea, which is 1.33 × as long as wide, 0.25 × as long as body of sternite, distinctly margined, and located anterad of center. Sternite VIII as in Figure 61. Aedeagus as in Figures 71 and 83.

Female. Length 1.67 mm. Body 2.48 × as long as broad. Vertex flattened; frontoclypeal ridge simple. Pronotum 0.88 × as long as broad; anterior edge as in male. Elytra 1.67 × as long as broad and 2.04 × as long as pronotum. Protibia with outer apical angle weakly dentate. Sternite III without pubescent fovea.

Variation. Pronotum yellowish orange to dark reddish brown, usually reddish brown. Elytra yellowish to yellowish brown, usually yellowish brown. Apex of pronotum in larger males weakly emarginate at midline. Size and dimensions vary as follows in a series of 13 males and 13 females from Preston, Ohio (Lot 1960 JFL):

TL mm: ♂ 1.50–1.75 (1.64 ± 0.021),
♀ 1.50–2.07 (1.73 ± 0.051);
TL/EW: ♂ 2.37–2.52 (2.45 ± 0.011),
♀ 2.44–2.61 (2.51 ± 0.012);
PL/PW: ♂ 0.84–0.92 (0.88 ± 0.008),
♀ 0.84–0.89 (0.87 ± 0.004);
EL/EW: ♂ 1.59–1.67 (1.62 ± 0.007),
♀ 1.65–1.78 (1.70 ± 0.010);
EL/PL: ♂ 1.91–2.05 (1.97 ± 0.014),
♀ 2.00–2.16 (2.09 ± 0.017);
GD/EW: ♂ 0.73–0.79 (0.76 ± 0.005),
♀ 0.76–0.82 (0.78 ± 0.005).

Total size range in material examined: 1.30–2.10 mm.

Paratypes. KENTUCKY: 3, Crittenden, Grant Co., Aug. 3, 1907, Lot 1962 JFL (C. G. Lloyd, coll.), ex *Polyporus robiniophilus* (herbarium specimen, C. G. Lloyd No. 41030) [JFL]; MARYLAND: 3, Plummers Island, Montgomery Co., April 29, 1905, Lot 1961 JFL (H. S. Barber, coll.), ex *Polyporus robiniophilus* (herbarium specimen, C. G. Lloyd No. 39777) [JFL, USNM]; OHIO: 65, Preston, Hamilton Co., Lot 1960 JFL (A. P. Morgan, coll.), ex *Polyporus robiniophilus* (herbarium specimen, C. G. Lloyd No. 41039 [FMNH, JFL, MCZ, USNM].

Distribution. Known only from Maryland, Kentucky, and Ohio.

Host fungi. Polyporus robiniophilus [3(1)].

Discussion. This species is characterized by the long and narrow body form; vesti-

ture of short, stout bristles; single and confused elytral punctation, which is relatively fine and sparse; narrow, crenulate, lateral pronotal margins; and, distinctly dentate protibial apex. In *Cis festivulus*, the protibial apex is rounded and the elytral bristles are uneven in length. *C. stereophilus* is somewhat shorter and broader with subseriate elytral punctation. In *Cis creberrimus* the body is more flattened and the elytral bristles longer and acute. Individuals of *Cis hystriculus* and *C. angustus* have coarser and denser punctation and longer bristles. In *Dolichocis indistinctus*, the body is long and narrow and the bristles short and stout, but in that species the antennae are 9-segmented and the protibial apex rounded.

Cis robiniophilus is a member of the *Cis fagi* group, which includes the North American *C. angustus* and the Palaearctic *Cis fagi* Waltl and *C. castaneus* Mellié.

The name *robiniophilus* is derived from *Robinia*, the generic name for certain of the locust trees, and the Greek *phileo*, to be fond of (referring to the occurrence of this beetle in fruiting bodies of *Polyporus robiniophilus*).

Cis rotundulus NEW SPECIES
Figure 41

Holotype. ♂, SOUTH CAROLINA: Walterboro, Colleton Co., II–15–64, H. Blocker [MCZ No. 31692]. Allotype, ♀, same data [MCZ].

Male. Length 1.50 mm. Body 1.93 × as long as broad, strongly convex. Head and pronotum dark reddish, elytra black. Vestiture of long, fine, recurved, yellowish hairs. Vertex slightly convex; frontoclypeal ridge bearing 2 lateral horns, which are about 3.0 × as long as wide at base, 0.20 × as long as pronotum, and separated by 4.0 basal widths, with lateral and mesal edges subparallel and apices slightly converging. Antennal segment III 1.60 × as long as IV. Pronotum 0.83 × as long as broad, widest at posterior third; anterior edge strongly produced and emarginate, forming 2 approximate, sharp, subtriangular horns, which are 0.10 × as long as pronotum; sides strongly rounded, the margins narrow and distinctly crenulate, not visible for their entire lengths from above; anterior angles barely produced forward, subacute; disc strongly convex, even; surface smooth and shiny; punctures 0.30 × as large as scutellar base and separated by 0.25 to 0.50 diameter. Elytra 1.16 × as long as broad and 1.50 × as long as pronotum; sides strongly rounded, apices acute; punctation single and confused; punctures coarser than and not as dense as those on pronotum, each puncture bearing a fine, recurved, yellowish hair, which is about 2.0 × as long as scutellar base. Prosternum strongly tumid and carinate; intercoxal process 0.40 × as wide as a procoxal cavity, parallel-sided. Protibia with outer apical angle strongly produced and dentate (Fig. 51). Metasternum 0.35 × as long as wide; suture 0.20 × as long as median length of sternum. Abdominal sternite III bearing a median, raised, circular, pubescent fovea, which is 0.33 × as long as body of sternite, distinctly margined, and located posterad of center.

Female. Length 1.50 mm. Body 1.82 × as long as broad. Vertex as in male; frontoclypeal ridge simple. Pronotum 0.73 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.15 × as long as broad and 1.73 × as long as pronotum. Protibial apex only slightly produced, angulate or weakly dentate. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to dark reddish, usually reddish. Elytra yellowish to black, usually dark brown or black. Frontoclypeal ridge on smaller males bearing 2 short, subtriangular processes; in larger males these are represented by longer, narrow horns, which may be 0.33 × as long as pronotum. Anterior edge of pronotum in small males barely produced and emarginate, forming 2 small tubercles; pronotal horns in larger specimens may be 0.20 × as long as pronotum. Size and di-

mensions vary as follows in a series of 18 males and 14 females from Walterboro, South Carolina:

TL mm: ♂ 1.27–1.77 (1.43 ± 0.028), ♀ 1.12–1.57 (1.37 ± 0.034);
TL/EW: ♂ 1.76–1.97 (1.87 ± 0.013), ♀ 1.78–1.93 (1.84 ± 0.011);
PL/PW: ♂ 0.74–0.91 (0.82 ± 0.011), ♀ 0.73–0.81 (0.78 ± 0.006);
EL/EW: ♂ 0.07–1.20 (1.14 ± 0.007), ♀ 1.12–1.21 (1.17 ± 0.008);
EL/PL: ♂ 1.44–1.75 (1.55 ± 0.021), ♀ 1.67–1.87 (1.77 ± 0.016);
GD/EW: ♂ 0.71–0.79 (0.75 ± 0.005), ♀ 0.70–0.77 (0.74 ± 0.006).

Total size range in material examined: 1.10–1.78 mm.

Paratypes. ALABAMA: 1, Mobile, II–17–12, H. P. Löding [CIN]; 1, same locality, 3–4–12 [CIN]; 3, Oak Grove, 17.6, Collection H. Soltau [USNM]. ARKANSAS: 1, Pine Bluff, 23.11, Collection H. Soltau [USNM]. FLORIDA: 3, Crescent City, Coll. Hubbard & Schwarz [USNM]; 2, Enterprise, May 27 [MCZ]; 2, same locality, 27.5, Hubbard & Schwarz [USNM]; 1, same locality, 28.5, Hubbard & Schwarz [USNM]; 2, 4 mi. SE Lake Placid, Highlands Co., June 25, 1965, Lot 1516 JFL, ex *Polyporus iodinus* [JFL]; 2, St. Nicholas [USNM]. GEORGIA: 1, Savannah, Chatham Co., Apr. 6, 1966, Lot 1810 JFL (H. and A. Howden, coll.), ex *Polyporus gilvus* [JFL]. LOUISIANA: 2, Fontainebleau State Park, St. Tammany Par., June 19, 1965, Lot 1456 JFL, ex *Ganoderma lucidum* [JFL]. MISSISSIPPI: 2, Hancock Co., 23.8, Hubbard & Schwarz [USNM]; 2, "Rose's Bluff," Natchez Trace, Madison Co., 25–III–1959, cortical [USNM]. NORTH CAROLINA: 5, Atlantic Beach, Carteret Co., May 19, 1966, Lot 1885 JFL (Carl Parsons, coll.), ex *Stereum ostrea* [JFL]; 2, Bladen Co., 2–V–1964, Jim F. Cornell [JFC]; 2, Moore Co., VI–1–64, J. F. Cornell [JFC]; 2, Raleigh, 25–IV–1964, Jim F. Cornell [JFC]; 2, same locality, IX–8–64, J. F. Cornell [JFC]; 15, Sampson Co., 2–V–1964, J. F. Cornell [JFC, JFL]; 1, Statesville, Tredell Co., May 25, 1966, Lot 1911 JFL (Carl Parsons, coll.), ex *Ganoderma curtisii* [JFL]; 2, same locality and date, Lot 1912 JFL (Carl Parsons, coll.), ex *Ganoderma curtisii* [JFL]. SOUTH CAROLINA: 30, Walterboro, Colleton Co., II–15–64, H. D. Blocker [FMNH, JFC, JFL, MCZ, USNM].

Distribution. Southeastern United States, from North Carolina to Florida and west to Arkansas and Louisiana (Fig. 89).

Host fungi. Ganoderma curtisii [2]; *Ganoderma lucidum* [1]; *Polyporus gilvus* [1]; *Polyporus iodinus* [1]; *Stereum ostrea* [1].

Discussion. This species resembles *Cis hirsutus* and *C. ursulinus* in the type of vestiture and frontoclypeal horns of the male. It differs from both in the shorter and broader form with narrowed elytral apices, reduced metasternum, and sharply carinate prosternum. In addition, *C. ursulinus* is usually more reddish in color with somewhat finer punctation, and *C. hirsutus* is larger with somewhat denser punctation.

Cis rotundulus is restricted to the southeastern United States and is not known from the West Indies. The narrowed elytral apices and shortened metasternum indicate that the species may be evolving in the direction of flightlessness; the hindwings are slightly reduced with a truncate apex. The distribution pattern suggests that *C. rotundulus,* like *C. ursulinus,* may have evolved on the mainland rather than in the Greater Antilles.

Cis stereophilus NEW SPECIES
Figure 40

Holotype. ♂, NORTH CAROLINA: Atlantic Beach, Carteret Co., May 19, 1966, Lot 1887 J. F. Lawrence (Carl Parsons, coll.), ex *Stereum* sp. on hardwood branch [MCZ No. 31693]. Allotype, ♀, same data [MCZ].

Male. Length 1.42 mm. Body 2.28 × as long as broad, moderately convex. Head and pronotum reddish orange, elytra blackish brown anteriorly, yellowish brown

posteriorly. Vestiture of short, stout, blunt, yellowish bristles. Vertex flattened, with slight median impression; frontoclypeal ridge bearing 2 sharp tubercles that are separated by about 2 basal widths. Antennal segment III 1.70 × as long as IV. Pronotum 0.87 × as long as broad, widest at posterior third; anterior edge strongly rounded, barely emarginate at midline; sides weakly rounded, the margins narrow and distinctly crenulate, not visible for their entire lengths from above; anterior angles barely produced forward, subacute; disc strongly convex, even; surface finely granulate and shiny; punctures 0.50 × as large as scutellar base and separated by 0.20 to 0.33 diameter. Elytra 1.44 × as long as broad and 1.71 × as long as pronotum; sides weakly rounded, apices blunt; punctation single and subseriate; punctures about as large and dense as those on pronotum, each bearing a stout, blunt, yellowish bristle, which is about 0.20 × as long as scutellar base. Prosternum slightly tumid; intercoxal process 0.22 × as wide as a procoxal cavity, narrowing posteriorly. Protibia with outer apical angle slightly produced and weakly dentate (Fig. 53). Metasternum 0.50 × as long as wide; suture 0.30 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.30 × as long as body of sternite, distinctly margined, and located anterad of center. Sternite VIII as in Figure 66. Aedeagus as in Figures 77 and 82.

Female. Length 1.30 mm. Body 2.17 × as long as broad. Vertex as in male; frontoclypeal ridge simple. Pronotum 0.84 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.42 × as long as broad and 1.89 × as long as pronotum. Protibia with outer apical angle slightly produced and angulate. Sternite III without pubescent fovea.

Variation. Pronotum yellowish orange to black, usually reddish orange. Elytra yellowish to black, usually blackish brown anteriorly and yellowish brown posteriorly. Almost all specimens examined were either bicolored with a paler pronotum or tricolored with the elytra yellowish posteriorly; in only one specimen was the coloration uniform. Frontoclypeal tubercles in males vary somewhat in size. Anterior edge of pronotum simple and rounded in smaller males, distinctly emarginate in larger specimens. Size and dimensions vary as follows in a mixed series of 13 males and 21 females from various parts of the Atlantic Coast:

TL mm: ♂ 1.20–1.50 (1.34 ± 0.025),
♀ 1.17–1.57 (1.37 ± 0.026);
TL/EW: ♂ 2.22–2.32 (2.27 ± 0.010),
♀ 2.17–2.42 (2.27 ± 0.014);
PL/PW: ♂ 0.84–0.92 (0.87 ± 0.006),
♀ 0.83–0.95 (0.87 ± 0.006);
EL/EW: ♂ 1.43–1.52 (1.46 ± 0.007),
♀ 1.42–1.58 (1.50 ± 0.010);
EL/PL: ♂ 1.71–2.00 (1.82 ± 0.021),
♀ 1.75–2.06 (1.93 ± 0.016);
GD/EW: ♂ 0.74–0.84 (0.77 ± 0.008),
♀ 0.71–0.81 (0.76 ± 0.006).

Total size range in material examined: 1.05–1.60 mm.

Specimens from northern Mexico differ from those of the eastern United States in being consistently smaller and darker in color and in having less well-developed frontoclypeal tubercles in the male.

Paratypes. DISTRICT OF COLUMBIA: 3, Washington, 24.5, Coll. Hubbard & Schwarz [USNM]. FLORIDA: 2, Torreya State Park, Liberty Co., Apr. 8, 1969, Lot 2712 JFL (S. B. Peck, coll.), ex *Stereum ostrea* [JFL]. MARYLAND: 1, Blad[e]-nsb[er]g, 13.7, Coll. Hubbard & Schwarz [USNM]; 1, same locality, 20.7, Coll. Hubbard & Schwarz [USNM]. MASSACHUSETTS: 3, Naushon Is., Elizabeth Islands, May 25, 1965, Lot 1671 JFL (Carl Parsons, coll.), ex *Stereum ostrea* [JFL, MCZ]; 2, Vineyard Haven, Martha's Vineyard, Dukes Co., May 20, 1965, Lot 1684 JFL (Carl Parsons, coll.), ex *Stereum ostrea* [MCZ];

1, Woods Hole, Barnstable Co., June 5, 1966, Lot 1812 JFL, ex *Stereum ostrea* [JFL]; 1, same locality and date, Lot 1813 JFL, ex *Stereum ostrea* [JFL]. NEW JERSEY: 2, Anglesea, 7.3, Coll. Hubbard & Schwarz [USNM]; 3, same locality, 24.7, Liebeck Collection [MCZ]. NORTH CAROLINA: 6, Atlantic Beach, Carteret Co., May 19, 1966, Lot 1887 JFL (Carl Parsons, coll.), ex *Stereum* sp. [JFL, MCZ]; 1, Highlands, Macon Co., June 16, 1962, Lot 146 R. C. Graves, ex *Stereum fasciatum* [= *S. ostrea*] [JFL]; 1, nr. Magnolia, Duplin Co., V–26–64, J. Cornell & P. Mampe [JFC]; 5, Raleigh, IX–27–64, J. F. Cornell, coll. [JFC, JFL]; 1, Thompson River Gorge, Transylvania Co., May 17, 1967, Lot 2498 JFL (Carl Parsons, coll.), ex *Stereum ostrea* [JFL]; 24, same locality, May 19, 1967, Lot 2511 JFL (Carl Parsons, coll.), ex *Stereum ostrea* [CAS, FMNH, JFL, MCZ]; 1, Tryon, 1784c Hopk. U. S., *Quercus*, W. F. Fiske [USNM]. NUEVO LEÓN: Chipinque Mesa, 5400′, Monterrey, June 23, 1969, Lot 3050 JFL (S. & J. Peck, coll.), ex *Stereum* sp. [JFL, MCZ]. PENNSYLVANIA: 1, Wisahick[o]n Cr., 7.24, Liebeck Collection [MCZ]; 1, Ches[t]n[u]t H[i]ll, VII.31, Liebeck Collection [MCZ].

Distribution. Eastern coast of the United States, from southern Massachusetts to northern Florida, and northeastern Mexico.

Host fungi. Stereum ostrea [10(5)]; *Stereum* sp. [2(2)].

Discussion. This species is characterized by the small size, moderately elongate form, single, subseriate, elytral punctation with very short and broad, blunt bristles, dentate or angulate protibial apex, coarsely and densely punctate pronotum with narrow lateral edges, and the normally light colored pronotum and bicolored elytra. The male has two tubercles on the frontoclypeal ridge. The species resembles *C. krausi* in several respects, but may be distinguished from it by the shorter body form (EL/EW less than 1.60), the single and more regular elytral punctation, and the coloration. *C. subtilis* differs from *C. stereophilus* in having distinctly dual elytral punctation, colorless bristles, finer and sparser pronotal punctation, uniform coloration, and in the absence of a pubescent fovea on the abdomen of the male. *C. festivulus* has a similar body form and blunt yellowish elytral bristles, but the punctation is confused, the bristles uneven, and the protibial apex rounded. *C. robiniophilus* also has similar body form and vestiture, but the pronotal punctation is much finer and sparser and the elytral punctures are uniform. Elytral bristles in *C. hystriculus* and *C. angustus* are not as short and broad and are more sparsely distributed; in addition, the former is much larger in size and lacks an abdominal fovea in the male, and the latter species is characterized by having sparser pronotal punctation.

In collections, individuals have been identified as *C. julichi* Dury, but the type of *julichi* is conspecific with *C. subtilis* Mellié.

This is the only species of North American Ciidae that is restricted to fungi of the genus *Stereum*, particularly *S. ostrea*. Fruiting bodies of this fungus are very thin and become woody with age, yet several insects are able to feed within the tissue. *C. stereophilus* definitely breeds in the fungus, and larvae have been taken on several occasions. It is rather rare in collections, but this is almost certainly due to the peculiar habitat. Specimens are known only from the Atlantic Coast and parts of northeastern Mexico, but it is likely that the species occurs throughout the eastern part of North America.

At the present time this species cannot be placed in any group, although it may be related to *C. krausi* and its relatives. It does not appear to have any relatives in the Palaearctic Region, and may be a northern representative of a Neotropical complex.

The name *stereophilus* is derived from the the basidiomycete genus *Stereum* and the Greek *phileo,* meaning to be fond of

(referring to the preference of these beetles for *Stereum* fruiting bodies).

Cis striolatus Casey

Cis striolata Casey, 1898: 79. Type locality: "Colorado (Salida)." Holotype, ♀, Casey Coll., USNM.
Cis fraterna Casey, 1898: 80. Type locality: "Utah (southwestern)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.
Cis macilenta Casey, 1898: 80. Type locality: "California (Lake Tahoe)." Holotype, ♀, Casey Coll., USNM. NEW SYNONYMY.
Cis versicolor Casey. — Hatch, 1962: 231. Misidentification.

Distribution. Widespread across the northern part of North America from the northern part of the Mackenzie District, Northwest Territory (not on map), to Nova Scotia, south into the Sierra Nevada and Rocky Mountains, in the Midwest as far as Kansas, and on the Atlantic coast as far as northern Florida (Fig. 101). Marginal records: NORTHWEST TERRITORY: Aklavik, Mackenzie District; BRITISH COLUMBIA: Midday Valley, Merritt; QUEBEC: Gaspé; NOVA SCOTIA: Portaupique; VIRGINIA: Mt. Vernon, Fairfax Co.; FLORIDA: Panama City, Bay Co.; KANSAS: Lawrence, Douglas Co.; COLORADO: Salida, Chaffee Co.; UTAH: Southwestern; CALIFORNIA: 21 mi. NE Strawberry, Toulumne Co.

Host fungi. Polyporus abietinus [6(2)]; *Polyporus pargamenus* [4(3)]; *Daedalea unicolor* [1(1)]; *Polyporus hirsutus* [1(1)].

Discussion. Individuals of this species may be distinguished from most other *Cis* by the narrow and elongate, somewhat depressed form, dual and distinctly seriate elytral punctation, vestiture of short, stout bristles, angular or dentate protibial apex, and slightly produced anterior pronotal angles. *Cis fuscipes* is larger and broader, with the anterior pronotal angles distinctly produced and the pronotal disc impressed anteriorly in the male. *C. cayensis* is smaller in size, with dual vestiture (visible only under higher magnification) and two tubercles on the vertex in the male. *C. striolatus* differs from *C. versicolor* in having a darker, duller, and more distinctly granulate pronotum with narrower lateral margins, the frontoclypeal ridge bituberculate in the male, and the abdominal fovea smaller. The species is most similar to *Cis tristis,* from which it differs by having a more sparsely punctate and coarsely granulate pronotum, yellowish elytral bristles, a much smaller abdominal fovea and different male genitalia (Fig. 70, cf. Fig. 69).

Cis striolatus appears to be most closely related to *Cis striatulus* Mellié from the Palaearctic Region and to *C. versicolor* from western North America. It is possible that *C. striatulus* and *C. striolatus* represent a single Holarctic species.

Cis striolatus, *C. fraterna,* and *C. macilenta,* all described by Casey, were based on a single female from Colorado, a pair from southwestern Utah, and a female from Lake Tahoe, California, respectively. Characters used to separate the three (impressions at the apical angles of the pronotum and the nature of the outer apical angle of the protibia) vary considerably within one series. The extent to which the apex of the protibia is produced, thereby forming a tooth, varies between the sexes, and the impressions at the anterior pronotal angles are found only in some larger males, in which the pronotum is laterally expanded.

The distribution pattern is a typically northern one, and the species is often associated with conifer forests. In the southeastern part of its range, *C. striolatus* is sympatric with *C. tristis. C. striolatus* normally feeds on the fruiting bodies of *Polyporus abietinus* and the related *P. pargamenus*, whereas *C. tristis* usually occurs on *P. versicolor* and its relatives. In western North America, *C. striolatus* may be sympatric with the related *C. versicolor;* the latter is associated with hardwoods and feeds on fruiting bodies of the *P. versicolor* group, while the former occurs on *P. abietinus* on conifers.

Cis subfuscus Gorham

Cis subfuscus Gorham, 1886: 357. Type locality: "Mexico, Cordova, Veracruz." Holotype, ♀, BMNH.

Distribution. Central Texas south along the eastern coast of Mexico to Veracruz. Marginal records: TEXAS: College Station, Brazos Co.; HIDALGO: 7 mi. SW Jacala; PUEBLA: 29 mi. E Xicotepec; VERACRUZ: Veracruz.

Host fungi. Polyporus hirsutus [2(1)]; *Panellus stypticus* [1(1)]; *Daedalea elegans* [1]. Also recorded from *Polyporus sanguineus.*

Discussion. This species is similar to *C. versicolor,* but the body is shorter and broader, the size is usually smaller, the elytral punctation is coarser and denser, and the male bears two tubercles on the frontoclypeal ridge. It also resembles *Cis pusillus* Gorham, described from the West Indies but occurring also in Brazil.

Cis subtilis Mellié

Cis subtilis Mellié, 1848: 353. Type locality: "Amérique boréale." Holotype, ♂, Marseul Coll., MNHN.
Cis confusus Blatchley, 1910: 899. Type locality: "... Perry ..." [Co., Indiana]. Lectotype, Blatchley Coll., PURD. NEW SYNONYMY.
Cis julichi Dury, 1917: 7. Type locality: "New York City." Holotype, ♂, Dury Coll., CIN. NEW SYNONYMY.
Cis wenzeli Dury, 1917: 8; Weiss and West, 1920: 8 (dist., biol.). Type locality: "Del.-[aware] Co. Penn." Holotype, Dury Coll., CIN. NEW SYNONYMY.

Distribution. Eastern North America, from New Hampshire south to Florida and west to Illinois, Arkansas, and eastern Texas (Fig. 106). Marginal records: NEW HAMPSHIRE: 5 mi. N Wilton, Hillsboro Co.; FLORIDA: 4 mi. NW Copeland, Collier Co.; TEXAS: Houston, Harris Co.; ARKANSAS: (southwest); ILLINOIS: Olive Branch, Alexander Co.

Host fungi. Polyporus pargamenus [33 (11)]; *Polyporus abietinus* [7(1)]; *Polyporus sector* [5(4)]; *Ganoderma applanatum* [1]; *Polyporus adustus* [1]; *Polyporus gilvus* [1]; *Stereum ostrea* [1].

Discussion. This species may be distinguished from other North American *Cis* by the relatively long and narrow body form, dual and confused elytral punctation, and vestiture of short, stout, colorless bristles. It differs from the closely related *C. acritus* by having two frontoclypeal tubercles and no abdominal fovea in the male. Within its range it may be confused with *C. tristis,* which differs in having the elytral punctation seriate. In *Cis stereophilus,* the elytral punctation is single and the bristles yellowish, while in *C. krausi* the elytra are more elongate (EL/EW greater than 1.60) and maculate.

Cis subtilis is fairly common throughout the eastern United States, where it breeds on the fruiting bodies of *Polyporus pargamenus* and its relatives. If one ignores secondary sexual characters, the species is barely distinguishable from the western *C. acritus* (*see* p. 443). The species has no close relatives in Europe and similar forms occur in the West Indies and Mexico.

Cis tetracentrum Gorham

Cis tetracentrum Gorham, 1886: 357. Type locality: "... Northern Sonora." Lectotype, ♂, BMNH.
Cis arizonae Dury, 1917: 5. Type locality: "Madera Canyon, Santa Rita Mountains, Arizona." Holotype, Wenzel Coll.? Paratypes, ♂ ♀, Dury Coll., CIN. NEW SYNONYMY.

Distribution. Mountains of southern California and Arizona and south through the Mexican highlands as far as central Veracruz (Fig. 94). Marginal records: CALIFORNIA: (no specific locality); ARIZONA: Graham Mt., Graham Co.; VERACRUZ: Orizaba; MEXICO: Toluca; DURANGO: 14 mi. SW El Salto; SONORA: (northern).

Host fungi. Polyporus versicolor [5(4)].

Discussion. This is the largest of the North American Ciidae, individuals averaging 3 mm in length. The form is somewhat elongate, the elytral punctation is moder-

ately coarse, dense, single, and confused, the vestiture consists of relatively long and fine bristles, the lateral pronotal margins are broad with a raised lip and barely crenulate edge, the anterior pronotal angles are produced and rounded, the prosternum is slightly tumid, and the male bears two stout pronotal horns, two subtriangular frontoclypeal plates, and a fairly small abdominal fovea (Fig. 32). In *Cis discolor* the body is more elongate and parallel-sided and the pronotal margins lack the raised lip and are distinctly crenulate. In *Cis vitulus* and *C. congestus* the body is shorter and broader, the bristles shorter and thicker, and the male lacks the abdominal fovea and bears an elevated, trisinuate ridge on the clypeus. In *Cis pistoria* the elytral punctation is dual and the bristles are very short and scalelike.

Cis tetracentrum is closely related to *Cis corticinus* Gorham, from the highlands of Mexico and Guatemala, and the two may not be specifically distinct. Individuals of *C. corticinus* are usually larger than those of *C. tetracentrum*, the elytral punctation is somewhat finer and denser, so that the vestiture is not as sparsely distributed, and the pronotal and clypeal horns in the male are more prominent. These two forms and *Cis pallidus* Mellié, from Brazil and Argentina, may constitute a species group, which, in turn, is related to the *Cis vitulus* complex, via *Cis bisbidens* Gorham.

Cis tridentatus Mannerheim

Cis tridentatus Mannerheim, 1852: 360. Type locality: "Insulae Sitkhae." Syntypes, Mannerheim Coll., MZUH.

Xestocis ednae Hatch, 1962: 232. Type locality: "Seattle, Wash." Holotype, ♂, Hatch Coll., UW. NEW SYNONYMY.

Xestocis reflexus Hatch, 1962: 232. Type locality: "Coupeville (Sunnyside), Wash." Holotype, ♂, Hatch Coll., UW. NEW SYNONYMY.

Distribution. Pacific Coast from southern Alaska, through British Columbia, Washington, and Oregon, to Monterey Co., California. Marginal records: ALASKA: Sitka; BRITISH COLUMBIA: Massett, Queen Charlotte Is.; WASHINGTON: White River, Mt. Rainier, Pierce Co.; CALIFORNIA: Big Sur, Monterey Co.

Host fungi. Fomes pinicola [10(7)]; *Poria cinerascens* [2(1)]; *Ganoderma oregonense* [1(1)]; *Polyporus sulphureus* [1(1)]; *Poria carbonica* [1(1)]; *Trametes sepium* [1(1)]; *Ganoderma applanatum* [1]; *Pleurotus ostreatus* [1]; *Polyporus gilvus* [1].

Discussion. This species is identical with *Cis americanus* in most respects but differs in having the elytral punctation obscurely dual, with the megapunctures barely larger than the micropunctures. *C. tridentatus* appears to be restricted to the immediate coast and no specimens have been taken inland. Throughout the range, it is sympatric with *C. americanus*, but the two have not been taken on the same host in any one area. *Cis tridentatus* is commonly found breeding in the fruiting bodies of *Fomes pinicola*, along with *Cis biarmatus* and *Dolichocis indistinctus*. *Cis americanus* ("*oweni*" type) also frequents *Fomes pinicola* but always at localities some distance from the coast and outside of the range of *C. tridentatus*. Coastal populations of *C. americanus* commonly breed in *Polyporus adustus*, *Stereum hirsutum*, and several other fungi (*see* p. 444).

Cis tristis Mellié

Cis tristis Mellié, 1848: 343. Type locality: "Nouvelle-Orléans." Holotype, ♀, Pic Coll. (Chevrolat Coll.), MNHN.

Cis setulosus Mellié, 1848: 257. Type locality: "Amérique boréale." Holotype, ♂, Melly Coll., GEN. NEW SYNONYMY.

Cis falli Blatchley, 1910: 898; Dury, 1917: 9 (dist.). Type locality: "Marion . . . " [Co., Indiana]. Lectotype, ♂, Blatchley Coll., PURD. NEW SYNONYMY.

Distribution. Eastern North America, from New York and Massachusetts south to Florida and west as far as southeastern Colorado and northeastern Mexico (Fig. 103). Marginal records: WISCONSIN: (no specific locality); MICHIGAN: Saugatuck, Allegan Co.; NEW YORK: (no specific

locality); MASSACHUSETTS: (no specific locality); FLORIDA: Panama City, Bay Co.; LOUISIANA: New Orleans, Orleans Par.; TEXAS: Brownsville, Cameron Co.; NUEVO LEÓN: Chorros de Agua, 13 mi. W Montemorelos; COLORADO: Pueblo, Pueblo Co.; NEBRASKA: Central City, Merrick Co.

Host fungi. Polyporus versicolor [3(3)]; *Lenzites betulina* [2(1)]; *Polyporus hirsutus* [2]; *Polyporus supinus* [2]; *Daedalea ambigua* [1(1)]; *Polyporus maximus* [1 (1)]; *Trametes hispida* [1(1)]; *Pleurotus* sp. [1]; *Polyporus cinnabarinus* [1].

Discussion. This species closely resembles *Cis striolatus* but may be distinguished from that species by the shiny pronotum with denser punctation, colorless elytral bristles, and larger abdominal fovea in the male. *Cis subtilis* is similar to *C. tristis* in the elongate form, dual elytral punctation, and colorless bristles, but the elytral punctation is confused and the abdominal fovea is absent.

The species is not very common, but it occurs throughout eastern North America, mainly south of New England and the Great Lakes, where it is usually found in association with *Polyporus versicolor* and its relatives. Although *Cis tristis* resembles the northern *C. striolatus*, as well as the European species *C. striatulus* Mellié and *C. comptus* Gyllenhal, the male genitalia are different and the true affinities may be with members of the Neotropical fauna.

Cis ursulinus Casey

Cis ursulina Casey, 1898: 83; Blatchley, 1910: 899 (dist.); Blatchley, 1918: 54 (dist.). Type locality: "Alabama." Holotype, ♀, Casey Coll., USNM.

Distribution. Southeastern United States, from North Carolina south to Florida and west to Arkansas and Louisiana (Fig. 92). Marginal records: NORTH CAROLINA: Knott's Island, Currituck Co. FLORIDA: Dunedin, Pinellas Co.; Archibold Biological Station, Highlands Co. LOUISIANA: Audubon State Park, West Feliciana Par. ARKANSAS: Hope, Hampstead Co. INDIANA: Crawford Co.

Host fungi. Ganoderma tsugae [1]; *Polyporus adustus* [1]; *Polyporus gilvus* [1]; *Polyporus sulphureus* [1]; *Polyporus versatilis* [1].

Discussion. This species differs from most North American *Cis* in having a vestiture of long, fine, recurved hairs, as in *C. hirsutus* and *C. rotundulus.* The form is more elongate than that of *C. rotundulus,* which also differs by virtue of the sharply carinate prosternum, narrowed elytral apices, shortened metasternum, and sparser punctation. Individuals of *C. hirsutus* are larger (TL more than 1.6 mm) and darker in color, with coarser punctation, smoother lateral pronotal margins, and a larger abdominal fovea in the male.

Like *C. rotundulus,* this species appears to be restricted to the southeastern United States. No specimens have been seen from the West Indies and the distribution indicates that the species may have evolved on the mainland.

Cis versicolor Casey

Cis versicolor Casey, 1898: 80. Type locality: "California (Calaveras . . . Co.)." Holotype, ♀, Casey Coll., USNM.

Cis dichrous LeConte, 1867: 58; Blaisdell, 1892: 34 (biol.); Weiss and West, 1921b: 169 (dist., biol.). Nomen nudum.

Distribution. Extreme southern Oregon, south throughout most of California, west of the Sierran crest, into Baja California Norte and east through Arizona into New Mexico and western Texas (Fig. 101). Marginal records: OREGON: 3 mi. W Dead Indian Springs, Jackson Co. CALIFORNIA: Dutch Flat, Placer Co.; Ash Mt. R., Sequoia National Park, Tulare Co. ARIZONA: 5 mi. SE Wickenburg, Maricopa Co. NEW MEXICO: San Juan Valley, Taos Co. TEXAS: Boquillas Camp, Big Bend National Monument, Brewster Co. BAJA CALIFORNIA NORTE: 12 mi. SE Maneandero.

Host fungi. Polyporus versicolor [22

(14)]; *Trametes hispida* [7(4)]; *Polyporus hirsutus* [5(2)]; *Lenzites betulina* [2(2)]; *Ganoderma brownii* [1]; *Polyporus cinnabarinus* [1]; *Schizophyllum commune* [1].

Discussion. This species is characterized by the elongate and somewhat depressed form, dual and distinctly seriate elytral punctation, vestiture of short bristles, shiny pronotum with fairly broad lateral margins, rounded or angulate protibial apex, reddish pronotum (in contrast to the dark elytra), and lack of frontoclypeal tubercles in the male. *Cis subfuscus* is somewhat smaller and not as elongate, with coarser and denser elytral punctation and distinct frontoclypeal tubercles in the male. *Cis striolatus* and *C. tristis* are similar, but in both, the outer apical angle of the protibia is more prominent, the lateral pronotal margins are narrower, and the clypeus of the male is tuberculate. *Cis subtilis* and *C. acritus* differ in having confused elytral punctation, while individuals of *C. fuscipes* are larger and broader with distinctly produced and rounded anterior pronotal angles and dentate protibial apices.

Cis versicolor appears to be related on the one hand to *C. striolatus* and *C. striatulus,* of the northern Nearctic and Palaearctic respectively, and on the other to *C. subfuscus* and *C. pusillus* of the Neotropical Region. The distribution is southwestern and the species probably extends into northern Mexico.

The species occurs on fungi of the *Polyporus versicolor* group, which are usually associated with hardwoods rather than conifers. In the wetter areas of central and northern California, it may be found with *C. vitulus*, *C. fuscipes*, *Sulcacis curtulus, Ceracis californicus,* and *Octotemnus laevis,* while in drier areas of the state it often occurs alone. In southeastern California and Arizona, *Cis versicolor* occupies two distinct habitats: along streams and river beds in the desert, where it feeds on fruiting bodies of *Trametes hispida* growing on cottonwoods, and in mountain canyons, where it may be found in *Polyporus versicolor* on various hardwoods. It has been collected in association with *Ceracis dixiensis* in the former and with *Cis tetracentrum* in the latter situation.

Cis vitulus Mannerheim

Cis vitulus Mannerheim, 1843: 299; Weiss, 1920b: 133–134 (biol.); Weiss, 1923: 199 (biol.); Weiss and West, 1921a: 61 (dist., biol.); Weiss and West, 1921b: 169 (dist., biol.). Type locality: "California." Types, Mannerheim Coll., MZUH ?

Cis caseyi Dalla Torre, 1911: 8, replacement name for *Cis illustris* Casey, 1898 (not Broun, 1880). NEW SYNONYMY.

Cis illustris Casey, 1898: 81. Type locality: "California (Humboldt Co.)." Holotype, ♀, Casey Coll., USNM.

Distribution. California, from Del Norte Co. to San Diego Co., and north central Arizona (Fig. 105). Marginal records: CALIFORNIA: Patrick Cr., Del Norte Co.; Dutch Flat, Placer Co.; Dorset Camp, Sequoia National Park, Tulare Co.; Palm Springs, Riverside Co.; San Diego, San Diego Co. ARIZONA: Oak Creek Canyon, Coconino Co.

Host fungi. *Polyporus versicolor* [29 (18)]; *Lenzites betulina* [4(3)]; *Polyporus adustus* [2(1)]; *Schizophyllum commune* [1].

Discussion. Individuals of this species are large and stout with single and uniform elytral punctation, vestiture of moderately short bristles, strongly tumid prosternum, broad lateral pronotal margins with a raised lip, produced and rounded anterior pronotal angles, and male with two pronotal horns, an elevated, trisinuate, frontoclypeal ridge (Fig. 3), and no abdominal fovea. *Cis laminatus* differs in the much narrower pronotal margins, shorter and broader form, coarser and denser pronotal punctation, and simple pronotal apex in the male. In *Cis tetracentrum,* the body is more elongate, the size is usually larger, the bristles are longer and finer, and the male bears two subtriangular frontoclypeal plates and an abdominal fovea. *Cis congestus* is quite similar to *C vitulus* but is

characterized by the smaller size, shorter and broader form, and coarser and denser pronotal punctation

Cis vitulus belongs to a group of species occurring mainly in the New World tropics and including the southeastern *C. congestus* and the Mexican species *C. bubalus* Reitter and *C. fasciatus* Gorham. The species has a relatively restricted range occurring primarily in mesic situations along the California coast and in the foothills of the Sierra Nevada.

Genus *Ennearthron* Mellié

Ennearthron Mellié, 1847: 110; Mellié, 1848: 360; Lacordaire, 1857: 552; Jacquelin du Val, 1861: 238; Thomson, 1863: 190; Abeille de Perrin, 1874b: 80; Reitter, 1902a: 59; Dalla Torre, 1911: 23; Winkler, 1927: 794; Miyatake, 1954: 55; Miyatake, 1959: 27; Lawrence, 1967b: 91–92; Lohse, 1965: 294. Type species, by subsequent designation, *Cis cornutus* Gyllenhal, 1827: 626 (Desmarest, 1860: 261).

Ennearthrum Bach, 1852: 111. Incorrect subsequent spelling.

Plesiocis Casey (in part). — Hatch, 1962: 233.

Included species. Ennearthron amamense Miyatake 1959: 27 [Ryukyu Is.]; *E. aurisquamosum* Lawrence, n. sp. [southeastern U. S., *see* p. 481]; *E. chujoi* Nakane and Nobuchi, 1955: 49 [Japan]; *Cis cornutus* Gyllenhal, 1827: 626 [Eurasia]; *E. ishiharai* Miyatake, 1954: 57 [Japan]; *E. mohrii* Miyatake, 1954: 56 [Japan]; *Plesiocis spenceri* Hatch [northwestern North America, *see* p. 482]. Total: 7 species.

Doubtfully included species. Ennearthron abeillei Caillol, 1914: 160 [southern Europe]; *Cis filum* Abeille de Perrin, 1874a: 53 [southern Europe]; *Ennearthron hayashii* Nobuchi, 1955: 108 [Japan]; *E. mussauense* Chujo, 1966: 529 [Bismark Is.]; *E. ondreji* Roubal, 1919: 63 [southeastern Europe]; *E. palmi* Lohse, 1966: 28 [northern Europe]; *E. poriae* Nakane and Nobuchi, 1955: 49 [Japan]; *Cis pruinosulus* Perris, 1864: 291 [Europe]; *E. pulchellum* Scott, 1926: 36 [Seychelles]; *E. reichei* Abeille de Perrin, 1874b: 89 [Egypt]; *Cis reitteri* Flach, 1882: 249 [Europe]. *See* discussion below.

Excluded species. Ennearthron argentinum Pic, 1916: 19 [Argentina]; *E. brevehirsutum* Pic, 1922: 8 [Cameroons]; *E. biroi* Pic, 1956: 77 [New Guinea]; *E. boettgeri* Reitter, 1880: 181 [New Zealand]; *E. longepilosum* Pic, 1922: 8 [India]; *E. multidentatum* Pic, 1917: 4 [China]; *E. obsoletum* Reitter, 1880: 182 [New Zealand]; *E. sinense* Pic, 1917: 4 [China]; *E. vianai* Pic, 1940: 12 [Argentina]. *See* discussion below.

Almost 60 species have been described in the genus *Ennearthron* on the basis of antennal segmentation (9 segments), and about half of these have already been transferred to other genera, such as *Ceracis, Diphyllocis, Dolichocis, Hadraule, Orthocis, Sulcacis,* and *Wagaicis*. The remainder may be divided into three groups: those definitely included in the genus as narrowly defined here, those doubtfully included for various reasons discussed below, and those excluded and transferred to the genus *Cis*.

The genus *Ennearthron* is used here in a restricted sense to include the seven species listed above and three or four others from India and China that are relatively small in size with a characteristic clypeal notch in the male (Fig. 8). They may be distinguished from *Plesiocis cribrum* by the broader intercoxal process of the prosternum, relatively longer metasternal suture, and the clypeal notch.

The doubtful species include four (*E. abeillei* Caillol, *E. mussauense* Chujo, *E. ondreji* Roubal, and *E. reichei* Abeille de Perrin) that have not been examined and are inadequately described, and seven more that seem to represent four separate lines:

1) *E. pulchellum* Scott. This is a broad and somewhat flattened form with bicolored elytra and vestiture of long, fine hairs. The intercoxal process of the prosternum is broad, the protibial apices are angulate, and there are no sexual orna-

ments on the head or pronotum of the male. It probably should be included in a distinct genus along with *Cis bifasciatus* Reitter from Japan and several undescribed Indo-Pacific species.

2) *E. filum* (Abeille de Perrin), *E. palmi* Lohse, and *E. hayashii* Nobuchi. These three species are all quite small (1.4 mm or less), narrow, and cylindrical, with dentate protibial apices and two small foveae on the head of the male.

3) *E. pruinosulum* (Perris) and *E. poriae* Nakane and Nobuchi. These two may be related to the last group, but they are larger in size and lack the dentate protibiae and pores on the head of the male.

4) *E. reitteri* (Flach). This species is short and broad with dual and indistinctly seriate elytral vestiture, carinate prosternum, broad lateral pronotal margins, and dentate protibial apices. It does not appear to be related to any of the above.

Nine species of *Ennearthron* were included on the basis of wrong antennal counts and should be transferred to the genus *Cis* (at least for the present). *Ennearthron biroi* Pic, *E. boettgeri* Reitter, and *E. obsoletum* Reitter belong to the *Cis pacificus* group (*see* Lawrence, 1967b: 98); *E. sinense* Pic and *E. brevehirsutum* Pic are probably related to *Cis fuscipes* Mellié; *E. vianai* Pic will eventually form part of a new genus; and each of the remaining forms belongs to a different group of *Cis*.

Key to the North American Species of *Ennearthron*

1. Elytral bristles longer, more than 0.33 × as long as scutellar base, subseriate; lateral pronotal margins visible for their entire lengths from above, the anterior angles produced and acute; apex of pronotum in male with 2 weak, approximate horns joined by an impressed ridge; British Columbia .... *E. spenceri* (p. 482)

— Elytral bristles shorter, less than 0.33 × as long as scutellar base, confused; lateral pronotal margins not or barely visible for their entire lengths from above, the anterior angles not or barely produced, almost right; apex of pronotum in male with 2 sharp, widely spaced horns; southeastern U. S. .... *E. aurisquamosum* (p. 481)

Ennearthron aurisquamosum NEW SPECIES

Holotype. ♂, NORTH CAROLINA: "N. C." "*aurisquamosus* Zimm." LeConte Collection [MCZ No. 31904]. Allotype, ♀, "N. C." [MCZ].

Male. Length 1.72 mm. Body 2.23 × as long as broad, strongly convex. Head and pronotum reddish, elytra dark reddish brown anteriorly, yellowish brown posteriorly. Vestiture of short, stout, blunt, yellowish bristles. Vertex with a deep, transverse impression, preceded by a median elevation; frontoclypeal ridge bearing 2 subtriangular plates with a median notch between them (Fig. 8). Antennal segment III 1.50 × as long as IV. Pronotum 0.87 × as long as broad, widest at posterior third; anterior edge produced and emarginate, forming 2 triangular horns that are separated by 1.75 basal widths; sides weakly rounded, the margins narrow and slightly crenulate, not visible for their entire lengths from above; anterior angles barely produced forward, almost right; disc strongly convex, even; surface finely granulate and shiny; punctures 0.20 × as large as scutellar base and separated by 0.25 to 0.35 diameter. Elytra 1.39 × as long as broad and 1.65 × as long as pronotum; sides weakly rounded, apices blunt; punctation single and confused; punctures slightly larger than and about as dense as those on pronotum, each bearing a stout, blunt, yellowish bristle, which is about 0.33 × as long as scutellar base. Prosternum biconcave; intercoxal process 0.30 × as wide as a procoxal cavity, parallel-sided. Protibia with outer apical angle strongly produced and dentate. Metasternum 0.46 × as long as wide; suture 0.33 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.27 × as long as body of sternite, distinctly margined, and located slightly posterad of center.

Female. Length 1.65 mm. Body 2.20 ×

as long as broad. Vertex with a slight median impression; frontoclypeal ridge simple. Pronotum 0.81 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.47 × as long as broad and 2.00 × as long as pronotum. Protibia with outer apical angle produced and weakly dentate. Sternite III without pubescent fovea.

Variation. Pronotum reddish orange to reddish brown. Elytra yellowish brown to almost black anteriorly, yellowish brown posteriorly, usually somewhat lighter at apices. Size and dimensions vary as follows in type series:

TL mm:	♂ 1.72, 1.82, 1.85,	♀ 1.65, 1.87;
TL/EW:	♂ 2.23, 2.28, 2.31,	♀ 2.20, 2.20;
PL/PW:	♂ 0.87, 0.90, 0.93,	♀ 0.81, 0.81;
EL/EW:	♂ 1.39, 1.44, 1.44,	♀ 1.44, 1.47;
EL/PL:	♂ 1.64, 1.65, 1.70,	♀ 1.88, 2.00;
GD/EW:	♂ 0.81, 0.84, 0.87,	♀ 0.82, 0.83.

Paratypes. KENTUCKY: 1, Mammoth Cave National Park, Edmonson Co., June 13, 1965, Lot 1430 JFL, ex *Polyporus adustus* [JFL]; NORTH CAROLINA: 3, "N. C." [JFL, MCZ].

Distribution. Kentucky and North Carolina.

Host fungi. Polyporus adustus [1].

Discussion. This species may be distinguished from *E. spenceri* by the narrower pronotal margins, shorter, confused elytral bristles, and more widely spaced pronotal horns. It resembles several species of *Cis* in general form and vestiture. *Cis stereophilus* has a more elongate form with subseriate elytral bristles, *C. laminatus* is somewhat larger with shorter and broader elytra, *C. castlei* is much smaller, and *C. duplex* has longer elytral bristles that are more sparsely distributed. The species most closely resembles an undescribed *Ennearthron* collected in *Polyporus volvatus* from western China.

Ennearthron spenceri (Hatch), NEW COMBINATION

Plesiocis spenceri Hatch, 1962: 233. Type locality: "Vancouver, B. C." Holotype, ♂, Hatch Coll., UW.

Distribution. Known only from Vancouver, BRITISH COLUMBIA. Probably introduced from Japan.

Host fungi. Recorded from *Polyporus volvatus.*

Discussion. This species may be distinguished from *E. aurisquamosum* on the basis of vestiture, pronotal margins, and male armature, as indicated in the key. It is also similar to several species of *Cis*, including *C. stereophilus, C. floridae,* and *C. duplex.* Both *Cis duplex* and *C. floridae* resemble *E. spenceri* in general form, punctation vestiture, and male armature, but both have 10-segmented antennae and in neither species is the frontoclypeal ridge interrupted in the middle. In addition, the vestiture in *C. floridae* is indistinctly dual and that of *C. duplex* is composed of shorter bristles. *Cis stereophilus* is similar in general form and color, but the bristles are much shorter and the male armature is different. In *Plesiocis cribrum,* the pronotal punctation is coarser and denser, the lateral pronotal margins are narrower, the clypeus of the male is quadridentate, and the prosternum and metasternum differ as indicated in the generic key.

Ennearthron spenceri belongs to a group of species inhabiting eastern Asia and including *E. amamense* Miyatake, *E. ishiharai* Miyatake, and *E. mohrii* Miyatake. Considering its limited distribution, the North American species may well be an introduction. Most of the individuals in the type series were taken from a herbarium specimen of *Polyporus volvatus* (origin not recorded), but at least one of the types in the University of British Columbia collection was taken in Vancouver at a later date than the herbarium series. Further collecting is needed to determine whether or not this species is established in southern British Columbia.

Genus *Dolichocis* Dury

Dolichocis Dury, 1919: 158; Lawrence, 1965: 289 (complete synonymy). Type species, by monotypy, *Dolichocis manitoba* Dury, 1919: 158.

Included species. Dolichocis indistinctus Hatch [northern North America, *see* p. 483]; *Cis laricinus* Mellié, 1848: 355 [Europe]; *Dolichocis manitoba* Dury [northern North America, *see* p. 483]; *Ennearthron yuasai* Chujo, 1941: 85 [Japan]. Total: 4 species.

Dolichocis represents a small aggregate of species with 9-segmented antennae, elongate, cylindrical form, and simple protibial apices. Like *Plesiocis,* it should be included within the genus *Ennearthron* as currently defined, but it is here retained as a distinct group, which has independently undergone antennal reduction. The genus is further discussed in a previous paper (Lawrence, 1965).

Key to the North American Species of *Dolichocis*

1. Pronotal punctation coarser and denser, the punctures more than 0.25 × as large as scutellar base and usually separated by less than 0.33 diameter; elytral punctures distinctly larger than pronotal punctures; elytral bristles 3 to 4 × as long as wide and about 0.33 × as long as scutellar base; vertex of male with median, raised, pubescent fovea; abdominal fovea of male margined and located in center of sternite III .... *D. manitoba* (p. 483)
— Pronotal punctation finer and sparser, the punctures less than 0.25 × as large as scutellar base and usually separated by more than 0.33 diameter; elytral and pronotal punctures subequal in size; elytral bristles 2 to 3 × as long as wide and about 0.17 × as long as scutellar base; vertex of male simple; abdominal fovea of male not margined and located anterad of center .... *D. indistinctus* (p. 483)

Dolichocis indistinctus Hatch

Dolichocis indistinctus Hatch, 1962: 234; Lawrence, 1965: 288. Type locality: "Stanley, B. C." Holotype, ♂, CAS.

Distribution. Known from scattered localities throughout the northern and montane parts of the continent, from the northern coast of British Columbia to the Gaspé Peninsula of Quebec and south into the Sierra Nevada, Chiricahua Mountains of southeastern Arizona, and the Green Mountains of Vermont. Marginal records: BRITISH COLUMBIA: Terrace; 36 mi. N Radium; QUEBEC: Mt. Lyall, 1500 ft.; VERMONT: Peru, Bennington Co.; COLORADO: 28 mi. NW Kremmling, Grand Co.; ARIZONA: Rustler Park, 8 mi. W Portal, Cochise Co.; CALIFORNIA: Caspar, Mendocino Co.; 6 mi. NW Fish Camp, Mariposa Co.

Host fungi. Fomes pinicola [6(3)]; *Trametes serialis* [2(2)]; *Fomes officinalis* [1].

Discussion. This species may be distinguished from *D. manitoba* by the finer pronotal punctation, shorter and stouter bristles, and simple vertex in the male. The only species of *Cis* likely to be confused with *D. indistinctus* is *C. robiniophilus,* in which the antennae are 10-segmented, the protibial apex produced and dentate, the bristles somewhat longer, and the surface shinier.

Dolichocis indistinctus is closely related to and probably conspecific with *Cis laricinus* Mellié, which is included in the genus *Ennearthron* by European workers (*see* p. 480). Its range is broadly sympatric with that of *C. manitoba* and it occurs on the same fungi, but *C. indistinctus* appears to be much rarer.

Dolichocis manitoba Dury

Dolichocis manitoba Dury, 1919: 158; Criddle, 1921: 80 (dist.); Weiss and West, 1921a: 61 (dist., biol.); Hatch, 1962: 233, pl. 48, fig. 6, 6a (dist.); Lawrence, 1965: 288; Pielou, 1966: 1235 (dist., biol.); Pielou and Matthewman, 1966: 1310 (dist., biol.); Pielou and Verma, 1968: 1284 (dist., biol.). Type locality: "Aweme, Manitoba." Holotype, ♀, Dury Coll., CIN.

Distribution. Northern and montane regions of North America, from the northern coast of British Columbia to New Brunswick and south to the central California coast, the southern Sierra Nevada, southeastern Utah, and northern Pennsylvania (Fig. 92). Marginal records: BRITISH CO-

LUMBIA: Terrace; ALBERTA: Edmonton; NORTHWEST TERRITORY: Fort Smith; MANITOBA: Victoria Beach; NEW BRUNSWICK: Matapedia; PENNSYLVANIA: Twin Lakes, Pike Co.; WISCONSIN: Minocqua, Oneida Co.; SOUTH DAKOTA: Black Hills, Harney Nat. For., Pennington Co.; COLORADO: 28 mi. N Kremmling, Grant Co.; UTAH: Wickiup Pass, 9000′, Henry Mts., Garfield Co.; CALIFORNIA: Huntington Lake, Fresno Co.; Ben Lomond, Santa Cruz Co.

Host fungi. Fomes pinicola [50(21)]; *Polyporus betulinus* [5(3)]; *Polyporus pargamenus* [4]; *Fomes annosus* [3(2)]; *Daedalea unicolor* [2(1)]; *Fomes officinalis* [1(1)]; *Ganoderma applanatum* [1(1)]; *Polyporus sulphureus* [1(1)]; *Fomes fomentarius* [1]; *Polyporus adustus* [1]; *Polyporus tulipiferae* [1]; *Polyporus volvatus* [1].

Discussion. This species is easily distinguished from *D. indistinctus* by the coarser punctation, longer and finer bristles, and fovea on the head of the male. It may be confused with *Sulcacis curtulus,* which has similar punctation and vestiture, but in that species the form is somewhat less elongate (EL/EW less than 1.50), the antennae are 10-segmented, and the apex of the protibia is expanded, rounded, and spinulose. *Cis hystriculus* and *C. angustus* are also somewhat similar, but the protibial apex is angulate or dentate, the antennae are 10-segmented, and the pronotum is not distinctly narrowed anteriorly.

Dolichocis manitoba is a common inhabitant of *Fomes pinicola* and its relatives in western North America, but in the eastern part of the continent it appears to have a broader host range.

Genus *Orthocis* Casey

Orthocis Casey, 1898: 84; Lawrence, 1965: 288 (complete synonymy). Type species, by subsequent designation, *Orthocis aterrima* Casey, 1898: 84 (= *Cis punctatus* Mellié, 1848: 337) (Lawrence, 1965: 288).

Cis (*Mellieicis*) Lohse, 1964: 122; Lawrence, 1965: 288. Type species, by original designation, *Cis alni* Gyllenhal, 1813: 386.

Cis (*Orthocis*) Casey, — Lohse, 1967: 285.

Included species. Cis abyssinicus Guerin-Meneville, 1847: 325 [Ethiopia]; *Cis aequalis* Blackburn, 1888: 268 [Australia]; *Cis alni* Gyllenhal, 1813: 386 [Eurasia]; *Cis alnoides* Reitter, 1884: 120 [southeastern Europe]; *Ennearthron annulatum* Kraus, 1908: 80 [Cuba]; *Cis apicipennis* Pic, 1916: 5 [Brazil]; *Cis assimilis* Broun, 1880: 347 [New Zealand]; *Cis collenettei* Blair, 1927: 166 [Marquesas]; *Cis coluber* Abeille de Perrin, 1874a: 52 [Europe]; *Cis cylindrus* Gorham, 1886: 358 [Panama]; *Cis discoidalis* Pic, 1922: 1 [Cameroons]; *Cis flavipennis* Pic, 1923: 12 [Indo China]; *Cis guamae* Zimmerman, 1942: 49 [Guam]; *Orthocis huesanus* Kraus, 1908: 77 [Florida, *see* p. 485]; *Cis immaturus* Zimmerman, 1939: 346 [Hawaii]; *Cis insularis* Waterhouse, 1876: 177 [Rodriguez]; *Cis juglandis* Reitter, 1885: 208 [southeastern Europe]; *Cis lacernatus* Reitter, 1908: 121 [eastern Africa]; *Cis leanus* Blackburn, 1907: 285 [Australia]; *Cis linearis* Sahlberg, 1901: 10 [northern Europe]; *Orthocis longula* Dury, 1917: 13 [eastern U. S., *see* p. 486]; *Cis lucasi* Abeille de Perrin, 1874b: 62 [southern Europe, northern Africa]; *Cis m-nigrum* Champion, 1913: 161 [Mexico]; *Cis nigrosplendidus* Nobuchi, 1955: 105 [Japan]; *Cis ornatus* Reitter, 1877: 381 [Japan]; *Cis perrisi* Abeille de Perrin, 1874a: 53 [southern Europe]; *Orthocis platensis* Brèthes, 1922: 302 [Argentina]; *Cis pseudolinearis* Lohse, 1965: 179 [Europe]; *Orthocis pulcher* Kraus, 1908: 78 [Florida, *see* p. 486]; *Cis punctatus* Mellié, 1848: 337 [North America, *see* p. 486]; *Cis schizophylli* Nakane and Nobuchi, 1955: 47 [Japan]; *Cis sublacernatus* Scott, 1926: 24 [Seychelles]; *Cis subornatus* Wollaston, 1861: 140 [southern Africa]; *Cis testaceofasciatus* Pic, 1922: 2 [Guadeloupe]; *Ennearthron transversatum* Kraus, 1908: 79 [southeastern U. S., *see* p. 488]; *Cis undulatus* Broun, 1880: 347 [New Zea-

land]; *Cis wollastonii* Mellié, 1849: 86 [Madeira]; *Cis zoufali* Reitter, 1902b: 6 [southeastern Europe]. Total: 38 species.

The genus *Orthocis* was discussed at length in an earlier paper (Lawrence, 1965) and arguments were presented for affording the group generic rank. Lohse (1964, 1965, 1967) prefers to consider *Orthocis* as a subgenus of *Cis* and includes within it certain species that I would exclude, namely *Cis festivus* (Panzer), *C. pygmaeus* (Marsham), and *C. vestitus* Mellié. As it is here delimited, the genus consists of 38 described species and at least 30 undescribed forms from various parts of the world.

Members of the genus *Orthocis* are usually distinguished from other ciids by the elongate form, 10-segmented antennae, simple and rounded protibial apices (Fig. 45), vestiture of short and fine hairs, elytral suture with inflexed margin at apex (Fig. 38), single and confused elytral punctation, well-developed and somewhat flattened prosternum with a fairly broad intercoxal process (Fig. 22), and complete absence of horns or tubercles on the head or pronotum of the male. Some species have 9-segmented antennae (*O. annulatus, O. pallidus*), while others may be clothed with stouter bristles (*O. abyssinicus, O. coluber, O. lucasi*), and a few are broader (*O. collenettei*). Lack of male armature is universal in the group, and the few species of *Cis* that have simple protibial apices and resemble *Orthocis* in other ways, are characterized by having teeth or tubercles on the male clypeus. There is another type of secondary sexual character in *Orthocis*, however, that is not found in other groups of ciids. In a number of species, the clypeus of the male is covered with setae or hairs that are longer and denser than those on the surrounding parts of the head (Fig. 37). The inflexed elytral margin also occurs in *Strigocis*, but members of that genus have a carinate prosternum and spinose protibial apices.

Key to the North American Species of *Orthocis*

1. Antennae 9-segmented; elytra bicolored, black or dark brown with median, yellow, transverse band; pronotal punctation coarse and dense, punctures 0.25 × as large as scutellar base and separated by 0.33 diameter or less; lateral pronotal margins narrow, not visible for their entire lengths from above; TL 1.4 mm or less .... *O. transversatus* (p. 488)
— Antennae 10-segmented; without other characters in combination 2
2. Size smaller, TL less than 1.25 mm; pronotal punctation coarse and sparse, punctures about 0.50 × as large as scutellar base and separated by 0.50 diameter or more; lateral pronotal margins not visible for their entire lengths from above; elytra bicolored, brownish with median, yellow, transverse band .... *O. pulcher* (p. 486)
— Size larger, TL more than 1.25 mm; pronotal punctation finer or denser; elytra uniformly pigmented or lateral pronotal margins easily visible for their entire lengths from above 3
3. Lateral pronotal margins narrow, not visible for their entire lengths from above, diverging anteriorly and abruptly converging near apex, so that they appear angulate (Fig. 19); body elongate, TL/EW more than 2.65 and EL/EW more than 1.80 .... *O. longulus* (p. 486)
— Lateral pronotal margins broader, easily visible for their entire lengths from above, weakly rounded or subparallel, not angulate, with raised lip (Fig. 18); body shorter and broader, TL/EW less than 2.65 and EL/EW less than 1.80 4
4. Elytra bicolored, each elytron bearing 2 large, yellow spots, Florida Keys .... *O. huesanus* (p. 485)
— Elytra uniformly pigmented .... *O. punctatus* (p. 486)

Orthocis huesanus Kraus

Orthocis huesanus Kraus, 1908: 77, pl. 3, fig. 3; Lawrence, 1965: 283. Type locality: "Key West, Fla." Holotype, ♀, USNM.

Distribution. Known only from Key West, Monroe Co., FLORIDA.

Host fungi. Unknown.

Discussion. This species is quite similar to *O. punctatus* as it is here defined, differing mainly in the slightly flatter body and bicolored elytra. The general form and

coloration are also similar to *O. m-nigrum* (Champion) described from Mexico.

Orthocis longulus Dury

Orthocis longula Dury, 1917: 13; Lawrence, 1965: 283. Type locality: "Pennsylvania . . ." [Linglestown]. Holotype, ♀, Dury Coll., CIN.

Distribution. Known from scattered localities in the southeastern part of North America, from southern Pennsylvania to Florida and west to Kansas and the Gulf Coast of Texas and northeastern Mexico. Localities: PENNSYLVANIA: Linglestown, Dauphin Co. FLORIDA: Gainesville, Alachua Co.; Crescent City, Putnam Co.; Enterprise, Volusia Co.; Lakeland, Polk Co.; Dunedin, Pinellas Co. ALABAMA: Spring Hill, Mobile Co. MISSISSIPPI: Lucedale, George Co. LOUISIANA: Harahan, Orleans Par.; Belle Chasse, Plaquemines Par. KANSAS: (no specific locality). TEXAS: Columbus, Colorado Co.; Victoria, Victoria Co. TAMAULIPAS: Tampico.

Host fungi. Unknown.

Discussion. This species is unique among the North American Ciidae in the very long and narrow body form and the narrow and somewhat angulate lateral pronotal margins. Some specimens of *O. punctatus* have fairly narrow pronotal margins, but these are never angulate and the body is always shorter and broader than that of *O. longulus.* The species is most closely related to *O. cylindrus* (Gorham) from Panama.

Orthocis pulcher Kraus

Orthocis pulcher Kraus, 1908: 78, pl. 3, fig. 4; Lawrence, 1965: 283. Type locality: "Key West, Fla." Holotype, ♀, USNM.

Distribution. Southern Florida. Localities: FLORIDA: Punta Gorda, Charlotte Co.; Coconut Grove, Dade Co.; Key West, Monroe Co.

Host fungi. Unknown.

Discussion. This species is easily distinguished by the small size, elongate body form, narrow lateral pronotal margins, very large pronotal punctures, and bicolored elytra. It is very similar to *O. testaceofasciatus* (Pic) described from Guadeloupe, and the two species may be synonymous.

Orthocis punctatus (Mellié)

Cis punctatus Mellié, 1848: 337. Type locality: "Amérique boréale." Holotype, ♂, Marseul Coll., MNHN.

Orthocis punctata (Mellié), Casey, 1898: 84 (dist.); Cockerell and Fall, 1907: 185 (dist.); Blatchley, 1910: 899 (biol.); Dury, 1917: 13; Brown, 1931: 90 (dist.); Hatch, 1962: 231 (dist., biol.); Lawrence, 1965: 283.

Orthocis aterrima Casey, 1898: 84; Dury, 1917: 13; Lawrence, 1965: 283. Type locality: "California (Alameda Co.)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Distribution. Widespread across North America from the edge of the Beaufort Sea (Mackenzie District) to the Island of Newfoundland, south on the Pacific Coast to Santa Barbara, California, through the Rocky Mountains to northeastern New Mexico, into the Black Hills of South Dakota, and through the eastern and midwestern states from New England to Florida and west to Kansas and Texas. Marginal records: NORTHWEST TERRITORY: Reindeer Depot, Mackenzie District. ALBERTA: McMurray. MANITOBA: Winnipeg. ONTARIO: Biscotasing. NEWFOUNDLAND: Harmon Field. FLORIDA: Biscayne, Dade Co. TEXAS: Kerrville, Kerr Co.; Victoria, Victoria Co. KANSAS: Riley Co. SOUTH DAKOTA: Hill City, Custer Co. NEW MEXICO: Las Vegas Hot Springs, San Miquel Co. CALIFORNIA: Santa Barbara, Santa Barbara Co. This is probably a composite distribution, since two or more species may be involved (*see* discussion below).

Host fungi. Auricularia auricula [1(1)]. Collected beneath the bark of various trees, including species of *Pinus, Abies, Prunus, Quercus, Ricinus,* and *Fagus.* Also taken by beating branches and in "powdery fungus" and "shelf fungus."

Discussion. Orthocis punctatus, as it is

here delimited, is extremely variable and may represent a complex of two or more related species. It may be distinguished from other North American *Orthocis* by the 10-segmented antennae, uniform elytral coloration, and relatively broad lateral pronotal margins, which are raised at the edge to form a narrow lip (Fig. 18). The actual widths of the pronotal margins vary considerably, but they are never angulate as in *O. longulus* (Fig. 19).

Characters exhibiting the most noticeable variation are: 1) size and density of pronotal punctures, 2) widths of lateral pronotal margins, 3) shape and prominence of anterior pronotal angles, 4) type of pronotal surface sculpture, and 5) relative size of pronotum. A comparative study of the male genitalia has not been made and must await a more complete analysis of the genus *Orthocis*.

The pronotal punctation varies from fine and sparse to fairly coarse and dense. The punctures in some specimens are 0.08 × as large as the scutellar base and separated by more than 1 diameter, while in others they may be as much as 0.25 × as large as the scutellar base and separated by 0.20 diameter. Finer and sparser punctation is characteristic of western and northern populations.

Lateral pronotal margins may be relatively narrow and only barely visible from above or they may be quite broad and explanate. From above they may be rounded and convex, subparallel, or even slightly sinuate at middle. The anterior angles in some specimens are strongly projecting and rounded, while in others they are barely projecting and almost right. Specimens from the southeastern United States and the Gulf Coast of Texas usually have narrower pronotal margins and less prominent anterior angles. In some southern populations, the lateral margins may diverge slightly towards the apex of pronotum. Narrower lateral margins are usually correlated with coarser and denser punctation.

Surface sculpture may be coarsely granulate and dull to smooth and shiny. In specimens with coarser and denser punctation, the interspaces are usually smoother and shiny.

The length of the pronotum relative to that of the elytra exhibits considerable variation. EL/PL varies from 1.80 to 2.60. The larger pronotum is usually found in southern populations.

The total size is also variable in *O. punctatus*, TL ranging from 1.30 to almost 3.00 mm. Larger specimens are usually found in northern and western populations and the smallest individuals are from Florida and Texas.

There is little variation in vestiture, all specimens examined being clothed with very short and fine hairs. The coloration is also fairly uniform throughout the range. It is likely that two species are included among this material and a third may even be found in the southeastern collections. In specimens from the western and northern parts of the continent the size is larger, the pronotum smaller, dull, finely and sparsely punctate, and the lateral pronotal margins are broad and somewhat rounded, with prominent anterior angles. The type specimens of both *O. punctatus* and *O. aterrimus* are of this form. The second form may be found throughout the eastern and midwestern part of the continent and south to Florida and the Gulf Coast. This is more variable but usually has a larger prothorax, with a shiny, coarsely and densely punctate pronotum, narrower, subparallel lateral margins with less prominent anterior angles. Casey's concept of *O. punctatus* would be included here. Since little is known of the biology of either form and since they cannot be consistently distinguished from one another, I prefer to lump them under one name for the present.

Orthocis punctatus is most closely related to the Palaearctic species *O. alni* (Gyllenhal), *O. linearis* (Sahlberg), and *O. pseudolinearis* (Lohse), and the latter two differ

from *O. alni* in much the same way as the two forms above differ from one another (*see* Lohse, 1965, 1967).

Orthocis transversatus (Kraus), NEW COMBINATION

Ennearthron transversatum Kraus, 1908: 79, pl. 3, fig. 7; Lawrence, 1965: 283, 286. Type locality: "Crescent City, Fla." Holotype, ♀, USNM.

?*Ennearthron pallidum* Kraus, 1908: 79, pl. 3, fig. 6; Lawrence, 1965: 283. Type locality: "Haw Creek, Fla." Holotype, ♀, USNM (type lost). NOMEN DUBIUM.

Orthocis pulcher Kraus,—Blatchley, 1923: 19 (dist., biol.); Blatchley, 1928: 68 (dist., biol.). Misidentification.

Distribution. Southeastern United States, from southern Virginia to Florida and west to the Gulf Coast of Texas. Marginal records: VIRGINIA: Virginia Beach, Princess Anne Co.; FLORIDA: Dunedin, Pinellas Co.; TEXAS: Dallas, Dallas Co.; Columbus, Colorado Co.

Host fungi. Unknown. Bred from decaying rattan vines in Virginia. Collected by beating dead branches of *Quercus* and from a dead limb of "red-bay" in Florida.

Discussion. This species may be distinguished from other North American *Orthocis* by the 9-segmented antennae, small size, coarse and dense pronotal punctation, and bicolored elytra. It resembles certain small, bicolored *Cis*, such as *C. krausi*, *C. superbus* Kraus, and *C. atromaculatus* Pic, but in all of these the vestiture consists of stouter bristles rather than fine hairs, the antennae are 10-segmented, and the protibial apices are angulate or dentate. The type of Kraus's *Ennearthron pallidum* was lost and the description is inadequate: thus the name is doubtfully synonymized above and considered a *nomen dubium*. *O. transversatus* is closely related to *O. annulatus* (Kraus) from Cuba, which also has 9-segmented antennae and may not be specifically distinct.

Genus *Strigocis* Dury

Strigocis Dury, 1917: 18; Leng, 1920: 247; Arnett, 1962: 829. Type species, by monotypy, *Strigocis opacicollis* Dury, 1917: 20.

Cis Latreille (in part),—Mellié, 1848: 356; Abeille de Perrin, 1874b: 75; Reitter, 1878e: 33; Gorham, 1883: 222; Reitter, 1902a: 57; Dalla Torre, 1911: 6; Winkler, 1927: 793; Kevan, 1967: 143.

Rhopalodontus Mellié (in part),—Fowler, 1890: 212; Peyerimhoff, 1915: 26; Horion, 1951: 321; Nobuchi, 1960: 39.

Xestocis Casey (in part),—Casey, 1898: 86; Dury, 1914: 18–19; Leng, 1920: 247; Arnett, 1962: 829.

Entypus (*Entypocis*) Lohse (in part),—Lohse, 1964: 121.

Sulcacis (*Entypocis*) Lohse (in part),—Lohse, 1967: 284.

Sulcacis Dury (in part),—Lawrence, 1965: 277.

Included species. *Cis bicornis* Mellié, 1848: 356 [Europe]; *Cis bilimeki* Reitter [Mexico, *see* p. 490]; *Strigocis opacicollis* Dury [eastern North America, *see* p. 490]; *Xestocis opalescens* Casey [eastern North America, *see* p. 490]; *Rhopalodontus tokunagai* Nobuchi, 1960: 39 [Japan]. Total: 5 species.

In a previous paper (Lawrence, 1965), I included *Cis bicornis* Mellié in the genus *Sulcacis*, although specimens had not been seen at that time. *Rhopalodontus tokunagai* Nobuchi was tentatively placed in the same genus. Having examined specimens of *C. bicornis* and reviewed the description of *R. tokunagai*, I would now place both species in the North American genus *Strigocis*, originally proposed by Dury (1917) for *S. opacicollis*. Members of both genera are characterized by having the protibial apex spinose, but in other respects the groups are quite distinct and probably distantly related. The main differences between *Strigocis* and *Sulcacis* are listed in the table below.

In addition to the species mentioned above, *Strigocis* includes the North American *Xestocis opalescens* Casey, the Mexican *Cis bilimeki* Reitter, and at least three more undescribed forms from Central America. Members of this genus resemble

TABLE 4. DIFFERENCES BETWEEN *STRIGOCIS* AND *SULCACIS*.

Characters	Strigocis	Sulcacis
Vestiture	single confused fine hairs or bristles	dual confused or seriate bristles
Antennae	10-segmented	9- or 10-segmented
Prosternum (in front of coxae)	tumid to carinate and on same level as intercoxal process (Fig. 14)	concave or biconcave and on different level than intercoxal process (Fig. 15)
Intercoxal process of prosternum	parallel-sided	tapering behind
Pronotal hypomera	strigose	not strigose
Anterior angles of pronotum	angulate or produced (Fig. 14)	rounded and not produced (Fig. 15)
Lateral margins of pronotum	broader, usually visible from above	narrower, not visible from above
Anterior edge of pronotum in male	produced and emarginate, usually with 2 processes	simple and rounded
Frontoclypeal ridge in male	produced and emarginate	bearing 2 teeth or tubercles
Maxillary palps	short and stout	long and narrow
Elytral suture	with inflexed margin at apex (Fig. 38)	without inflexed margin
Metasternal suture	longer	shorter

various *Cis* species having a strongly tumid or carinate prosternum (*Cis tricornis* group or *Cis nitidus* group), but differ from them by virtue of the spinose protibial apex and inflexed elytral suture. Species of *Ceracis* have spinose protibial apices, but differ in having a concave prosternum with laminate intercoxal process, rounded anterior pronotal angles, and simple elytral suture.

Key to the North American Species of *Strigocis*

1. Vestiture of very short, stout bristles, which are less than 2.0 × as long as wide; pronotal punctation fine and dense, punctures less than 0.10 × as large as scutellar base and separated by less than 0.75 diameter; pronotal surface distinctly granulate and dull; abdominal fovea in male more than 0.60 × as long as body of sternite III; known from highlands of Mexico and probably occurring in southern Arizona .... *S. bilimeki* (p. 490)

— Vestiture of finer hairs; pronotal punctures separated by more than 0.75 diameter or punctures more than 0.15 × as large as scutellar base; abdominal fovea less than 0.60 × as long as body of sternite III; eastern United States and northern Mexico 2

2. Body shorter and stouter, EL/EW less than 1.33; elytral hairs colorless, less than 0.15 × as long as scutellar base and not or barely visible under 10× magnification; lateral margins of pronotum broader and with a raised lip; pronotal surface usually shiny .... *S. opalescens* (p. 490)

— Body longer and narrower, EL/EW more than 1.33; elytral hairs yellow, more than 0.20 × as long as scutellar base and easily

visible under 10× magnification; lateral margins of pronotum narrower and without raised lip; pronotal surface usually dull .... *S. opacicollis* (p. 490)

Strigocis bilimeki (Reitter), NEW COMBINATION

Cis bilimeki Reitter, 1878a: 33; Gorham, 1883: 222. Type locality: "Mexico." Lectotype, ♂, Oberthür Coll., MNHN.

Distribution. Mountains of northern Mexico; probably extending into southern Arizona. Marginal records: DURANGO: 11 mi. SW El Salto; HIDALGO: Tenango de Doria; TAMAULIPAS: Rancho del Cielo, 3700′, NW Gomez Farias.

Host fungi. Lenzites betulina [1(1)]; *Polyporus versicolor* [1].

Discussion. Individuals of this species are somewhat larger than those of *S. opacicollis* and *S. opalescens* (TL usually greater than 1.5 mm) and are easily distinguished by the short, stout, yellowish bristles, fine and dense pronotal punctation, dull surface, and large abdominal fovea in the male. The predicted occurrence of *S. bilimeki* in the Southwest is based on a collection from southern Arizona that was discarded because it was thought to be a contaminant population of *S. opacicollis*. Specimens and records were not retained, but I now think it is more likely that this "contaminant" collection was *S. bilimeki*, present in the original collection as a few larvae and thus overlooked. Further collecting in Arizona should verify this.

Strigocis opacicollis Dury

Strigocis opacicollis Dury, 1917: 20; Weiss and West, 1920: 8 (dist., biol.). Type locality: "Cincinnati, Ohio." Syntypes, Dury Coll., CIN.

Distribution. Eastern North America, from southern Vermont and New Hampshire to the Florida Keys, west as far as eastern Kansas, and south into Mexico (Fig. 100). Marginal records: NEW YORK: N. Fairhaven, Cayuga Co. VERMONT: Manchester, Bennington Co. NEW HAMPSHIRE: 7 mi. NW Wilton, Hillsboro Co. FLORIDA: Chipola Park, Dead Lake, Calhoun Co.; Plantation Key, Monroe Co. ARKANSAS: Washington Co. KANSAS: Onaga, Pottawatomie Co. NUEVO LEÓN: Chorros de Agua, 13 mi. W Montemorelos. HIDALGO: Tenango de Doria. VERACRUZ: 20 mi. E Cordoba; Orizaba.

Host fungi. Polyporus versicolor [29(14)]; *Lenzites betulina* [7(1)]; *Polyporus hirsutus* [5]; *Polyporus maximus* [1(1)]; *Polyporus pinisitus* [1(1)]; *Polyporus subectypus* [1(1)]; *Polyporus adustus* [1]; *Polyporus gilvus* [1]; *Polyporus sanguineus* [1]; *Polyporus tenuis* [1].

Discussion. This is the most common and widespread species of *Strigocis* in North America. It differs from *S. opalescens* in the more elongate form, narrower lateral pronotal margins, and the size and color of the hairs. It is similar to *S. bilimeki* in general form and male armature (frontoclypeal ridge and pronotal apex each forming an emarginate plate), but the vestiture is quite different and the pronotal punctation is much denser.

In eastern North America, *S. opacicollis* is sympatric with *S. opalescens*, and the two may feed on the same fungi; the latter species, however, appears to be much rarer. In northern Mexico, all three *Strigocis* occur in the same areas along with two undescribed species. All appear to frequent the same fungi (*Polyporus versicolor* and its relatives) and as many as three have been taken on the same fruiting body.

Individuals from Plantation Key differ from those to the north in being smaller in size (TL = 1.0 to 1.3 mm) with the pronotal surface shiny and reddish in color, contrasting with the blackish elytra. This may be a dwarf race or a distinct species. Specimens from Veracruz are somewhat similar.

Strigocis opalescens (Casey), NEW COMBINATION

Xestocis opalescens Casey, 1898: 86; Dury, 1917: 17 (dist.). Type locality: "Pennsylvania (Westmoreland Co.)" [St. Vincent]. Holotype, ♂, Casey Coll., USNM.

Xestocis davisi Dury, 1917: 16. Type locality: "Staten Island, N. Y." Holotype, ♂, Dury Coll., CIN. NEW SYNONYMY.

Distribution. Eastern North America, from southern Michigan and New York south and west as far as northeastern Mexico. Marginal records: MICHIGAN: Detroit, Wayne Co.; NEW YORK: Staten Is., Richmond Co.; NORTH CAROLINA: 2.5 mi. NW Highlands, Macon Co.; MISSISSIPPI: Meridian, Lauderdale Co.; TAMAULIPAS: Rancho del Cielo, 3700′, NW Gomez Farias.

Host fungi. Polyporus versicolor [3(1)].

Discussion. Individuals of this species are shorter, broader, and more rounded than those of either *S. opacicollis* or *S. bilimeki*, the lateral pronotal margins are broader and somewhat raised, and the vestiture consists of very short and fine, pale hairs. Although it occurs throughout eastern North America and into Mexico, *S. opalescens* appears to be rare and there are few specimens in collections.

Genus *Hadraule* Thomson

Hadraule Thomson, 1863: 182; Lawrence, 1965: 282 (complete synonymy); Lohse, 1967: 295. Type species, by monotypy, *Cis elongatulus* Gyllenhal, 1827: 627.

Maphoca Casey, 1900: 165. Type species, by monotypy, *Maphoca blaisdelli* Casey, 1898: 165. NEW SYNONYMY.

Maphcae Dalla Torre, 1911: 21. Incorrect subsequent spelling.

Diphyllocis Reitter, — Dury, 1917: 4; Leng, 1920: 247; Arnett, 1962: 829; Hatch, 1962: 235 (not Reitter, 1885: 209).

Pityocis Peyerimhoff, 1918: 141. Type species, by monotypy, *Pityocis coarctatus* Peyerimhoff, 1918: 142 (= *Cis elongatulus* Gyllenhal).

Ennearthron (*Knablia*) Roubal, 1936: 53. Type species, by monotypy, *Cis elongatulus* Gyllenhal.

Included species. Maphoca blaisdelli Casey [western North America, *see* p. 491]; *Cis elongatulus* Gyllenhal [Eurasia and northeastern North America, *see* p. 492]; *Hadraule explanata* Lawrence, n. sp. [northeastern North America, *see* p. 493]. Total: 3 species.

The only species currently included in the genus *Hadraule* is the type, *H. elongatula,* although several others have been added at one time or other (*see* Lohse, 1964 and Lawrence, 1965). Casey's *Maphoca blaisdelli* was placed in a separate genus because of the 2-segmented antennal club, and Dury (1917) transferred the species to *Diphyllocis* for the same reason. Actually, *M. blaisdelli* is similar to *H. elongatula* in several respects, including prothoracic structure (Fig. 28), and the two appear to be congeneric in spite of the slight reduction of the first club segment in the former. Reitter's genus *Diphyllocis,* on the other hand, is based on a distinct and unrelated European species, *D. opaculus* (Reitter). Members of *Hadraule* are easily recognized by the small size, flattened form, 9-segmented antennae, and elongate prosternum.

Key to the North American Species of *Hadraule*

1. Pronotum slightly narrowed apically, widest behind middle, the margins broad and explanate, easily visible for their entire lengths from above (Fig. 21); head strongly declined, only partly visible from above; size larger, TL more than 1.5 mm .... *H. explanata* (p. 493)
— Pronotum slightly broader apically, widest at anterior fourth, the margins narrow, not or barely visible for their entire lengths from above (Fig. 20); head only weakly declined, visible from above; size smaller, TL less than 1.5 mm 2
2. Antennal club apparently 2-segmented, the first club segment barely larger than the last funicular segment; pronotum reddish, much lighter in color than elytra .... *H. blaisdelli* (p. 491)
— Antennal club 3-segmented; pronotum and elytra uniformly dark in color .... *H. elongatula* (p. 492)

Hadraule blaisdelli (Casey), NEW COMBINATION

Maphoca blaisdelli Casey, 1900: 165; Lawrence, 1965: 279. Type locality: "California (Mokelumne Hill, Calaveras Co.)." Holotype, ♀, Casey Coll., USNM.

Diphyllocis blaisdelli (Casey), — Leng, 1920: 247; Criddle, 1926: 98 (dist.); Hatch, 1962: 235, pl. 48, fig. 8 (dist., biol.).

Distribution. Western North America, from southern British Columbia to southern California, east through Utah, Arizona, and New Mexico into Texas, and south into Mexico. Also known from Iowa, Ohio, Michigan, Massachusetts, Connecticut, and Florida. Marginal records: BRITISH COLUMBIA: Peachland; CALIFORNIA: 1.5 mi. NW Mt. Laguna, San Diego Co.; UTAH: Logan, Cache Co.; ARIZONA: 15 mi. E Douglas, Cochise Co.; NEW MEXICO: Deming, Luna Co.; TEXAS: San Antonio, Bexar Co.; VERACRUZ: San Juan de la Punta; IOWA: Iowa City, Johnson Co.; OHIO: Mt. Washington, Cincinnati, Hamilton Co.; MICHIGAN: Saugatuck, Allegan Co.; MASSACHUSETTS: Amherst, Hampshire Co.; CONNECTICUT: New Haven, New Haven Co.; FLORIDA: (no specific locality). Only one of the northeastern records (Saugatuck, Michigan) is known to be based on field collected specimens; the others are probably herbarium infestations (*see* below).

Host fungi. Lenzites saepiaria [3(2)]; *Polyporus adustus* [3(1)]; *Trametes sepium* [3]; *Polyporus munzii* [2]; *Polyporus versicolor* [2]; *Daedalea confragosa* [1(1)]; *Fomes annosus* [1(1)]; *Polyporus anceps* [1(1)]; *Polyporus biformis* [1(1)]; *Trametes hispida* [1(1)]; *Fomes robiniae* [1]. Also recorded from *Pleurotus* sp. and *Polyporus cuticularis.*

Discussion. This is the only widespread *Hadraule* in North America, the other two being restricted to the extreme northeastern part of the continent. The species may be distinguished from both *H. explanata* and *H. elongatula* by the 2-segmented antennal club and reddish prothorax.

H. blaisdelli is fairly common in California, where it breeds on several different fungi, and it extends throughout the Southwest and into southern Mexico. It has also been collected in Michigan and has been recorded as a herbarium pest from various localities in eastern North America. Specimens from Vancouver, British Columbia, were taken from a herbarium polypore and the Amherst specimens are from a lichen collection. In the National Fungus Collections at Beltsville, Maryland, a large number of dead specimens were found in various boxes of fungi, but there is reason to believe that this is an old infestation originating at the Missouri Botanical Garden. This is the only species of Ciidae that is known to be an herbarium pest.

Hadraule elongatula (Gyllenhal)

Cis elongatulus Gyllenhal, 1827: 627. Type locality: "Sparrsätra Westrogothiae" [Sweden]. Types, Gyllenhal Coll., Zool. Univ. Mus., Uppsala ?

Hadraule elongatula (Gyllenhal), — Thomson, 1863: 182.

Hadraula elongatula (Gyllenhal), — Pielou and Verma, 1968: 1184 (dist., biol.).

Ennearthron striatum J. Sahlberg, 1901: 11. Type locality: "Fennia australi" [Finland]. Types, C. Sahlberg Coll., MZUH ?

Pityocis coarctatus Peyerimhoff, 1918: 142. Type locality: "Ain-Haouas près Djelfa." [Algeria]. Lectotype, ♂, Peyerimhoff Coll., MNHN.

Cis elongatus Schilsky, 1900: 59. Incorrect subsequent spelling.

Distribution. Widespread throughout Europe, Siberia, and North Africa. In North America, known only from Ludlow, NEW BRUNSWICK. Probably introduced from Europe.

Host fungi. Polyporus betulinus [1(1)].

Discussion. This species may be distinguished from *H. blaisdelli* by the 3-segmented antennal club and darker pronotum. *H. explanata* is somewhat larger with broader pronotal margins. Smaller specimens of *Cis striolatus* and its relatives may be confused with *H. elongatula* but they differ in having 10-segmented antennae and a shorter prosternum in front of the procoxae.

Hadraule elongatula has been recorded from various parts of the Palaearctic Region, but there is only a single record from North America. Although the New Brunswick population may represent an introduction, it is possible that this small and elusive beetle occurs throughout Canada. In the Old World, *H. elongatula*

has been taken in the galleries of *Dorcatoma* (Anobiidae) in *Liriodendron*, in bark beetle galleries (Scolytidae) in *Picea*, in association with *Pinus halepensis* in North Africa, and on a birch fungus in Scandinavia (Reitter, 1878a; Peyerimhoff, 1918; Palm, 1946, 1952). This population was apparently breeding in the conks of *Polyporus betulinus*.

Hadraule explanata NEW SPECIES

Holotype. ♀, MAINE: E Machias, Washington Co., June, Fenyes Collection [CAS].

Female. Length 1.55 mm. Body 2.48 × as long as broad, flattened, GD/EW 0.68. Head and pronotum reddish brown, elytra yellowish brown. Vestiture of very short, erect, colorless, fine bristles. Vertex flattened; frontoclypeal ridge simple. Antennal club 3-segmented. Pronotum (Fig. 21) 0.78 × as long as broad, widest at posterior fourth; anterior edge weakly rounded; sides subparallel, barely sinuate at middle, slightly converging anteriorly, the margins broad and distinctly crenulate, easily visible for their entire lengths from above; anterior angles distinctly produced and rounded; disc slightly convex, even; surface distinctly granulate and dull; punctures 0.18 × as large as scutellar base and separated by 1.0 to 2.0 diameters. Elytra 1.76 × as long as broad and 2.44 × as long as pronotum; sides subparallel, apices blunt; punctation dual and distinctly seriate; megapunctures at least 2.0 × as large as pronotal punctures, separated by less than 0.50 diameter between and within rows, subquadrate, shallow, and nude; micropunctures located mainly between rows, each bearing a fine erect, colorless bristle, which is 0.20 × as long as scutellar base. Prosternum slightly tumid; intercoxal process 0.62 × as wide as a procoxal cavity, parallel-sided. Protibial apex narrowly rounded.

Distribution. Known only from the type locality.

Host fungi. Unknown.

Discussion. This species is easily distinguished from the other two *Hadraule* by the broad and explanate lateral pronotal margins; it is also somewhat larger in size. In general form the species resembles *Cis striolatus*, but the latter differs in having 10-segmented antennae, angulate or dentate protibia, and narrower lateral pronotal margins. At present only a single female specimen is known, but it is sufficiently distinct to warrant description at this time. It is hoped that further collecting in the Northeast will turn up the male and reveal something of the biology of this species.

The name *explanatus* is derived from the Latin word meaning to make level or flat (referring to the broad, explanate lateral pronotal margins).

Genus *Plesiocis* Casey

Plesiocis Casey, 1898: 87; Dalla Torre, 1911: 20; Dury, 1917: 22; Leng, 1920: 247; Arnett, 1962: 829; Hatch, 1962: 233. Type species, by monotypy, *Plesiocis cribrum* Casey, 1898: 87.
Ennearthron Mellié, — Hubbard, 1892: 254, 255.

Included species. Plesiocis cribrum Casey [western and northern North America, *see* p. 494].

Excluded species. Plesiocis spenceri Hatch (*see* p. 482).

This genus contains the single species *P. cribrum*, which probably should be lumped together with the heterogeneous assemblage of forms currently included in *Ennearthron* (*see* discussion on p. 480). I prefer to retain the genus *Plesiocis*, which has been consistently recognized by American authors, until a thorough generic revision is possible. The North American species of *Ennearthron* are easily distinguished from *Plesiocis cribrum* by the characters given in the generic key as well as by the smaller size and less robust body form. The narrow and parallel-sided intercoxal process of the prosternum is similar to that found in *Ceracis*, but the protibial apex bears a stout tooth as in species of *Cis*. Although the relationships of *P. cribrum* are obscure at present, there is little doubt that it repre-

sents an independent line exhibiting reduction in antennal segmentation.

Plesiocis cribrum Casey

Plesiocis cribrum Casey, 1898: 87; Dury, 1917: 21 (dist.); Criddle, 1921: 80 (dist.); Weiss, 1923: 199 (biol.); Weiss and West, 1922: 199 (dist., biol.); Hatch, 1962: 234, pl. 48, fig. 5, 5a (dist., biol.). Type locality: "California (Mokelumne Hill, Calaveras Co.)." Holotype, ♂, Casey Coll., USNM.

Distribution. Northern and montane regions of North America, from British Columbia to the Gaspé Peninsula of Quebec, south to the Laguna Mountains in California, the edge of the Colorado Plateau in Arizona and New Mexico, the Great Lakes Region, and the Shenandoah Mountains of Virginia (Fig. 89). Marginal records: BRITISH COLUMBIA: Salmon Arm; QUEBEC: Gaspé; VIRGINIA: Stokesville, Augusta Co.; MICHIGAN: East Tawas, Iosco Co.; WISCONSIN: (no specific locality); NEW MEXICO: 5 mi. W Luna, Catron Co.; ARIZONA: Williams, Coconino Co.; CALIFORNIA: 1.5 mi. NW Mt. Laguna, San Diego Co.

Host fungi. Polyporus volvatus [48(30)]; *Polyporus anceps* [8(5)]; *Polyporus alboluteus* [2].

Discussion. This species may be distinguished from most North American Ciidae by the 9-segmented antennae, fairly short and broad body form, dentate protibial apex, coarse and dense punctation which is single and confused on the elytra, vestiture of short, stout bristles, and 4 sharp teeth on the clypeus of the male (Fig. 4). *Cis laminatus* is similar but has 10-segmented antennae and a raised, trisinuate plate on the clypeus of the male. *Cis duplex* differs in antennal segmentation and male armature, and is usually smaller in size. *Dolichocis manitoba* has 9-segmented antennae and similar coarse punctation, but the body is elongate and cylindrical (EL/EW usually more than 1.50), the protibial apices are simple, and the male sexual characters are different. *Ennearthron spenceri* and *E. aurisquamosum* are both similar to *P. cribrum* in antennal segmentation, protibial apices, and general body form, but they differ from the latter in having a broader prosternal intercoxal process, longer metasternal suture, and distinctly notched clypeus in the male (Fig. 8).

Plesiocis cribrum is widespread and abundant throughout the coniferous forests of western North America and appears to be rare in the eastern part of the continent. It occurs primarily on the conks of *Polyporus volvatus* but also breeds in *P. anceps*. At the southern end of its range, it shares the same habitat with *C. duplex* and the latter apparently replaces *P. cribrum* in southern Arizona.

Genus *Ceracis* Mellié

Ennearthron (*Ceracis*) Mellié, 1848: 375; Lawrence, 1967b: 95 (complete synonymy). Type species, by subsequent designation, *Ennearthron* (*Ceracis*) *sallei* Mellié, 1848: 377 (Lawrence, 1967b: 95).

Included species. See Lawrence (1967b: 97–98). Also included are *Ceracis magister* Lawrence, n. sp. [Florida, *see* p. 498] and *C. pecki* Lawrence, n. sp. [southeastern U. S., *see* p. 499]. Total: 42 species.

This genus has been treated in a previous paper (Lawrence, 1967b) and need not be discussed in detail here. In the following section, two new species are described, one species (*C. similis*) is added to the fauna (although not actually recorded from the United States), new keys to males and females are presented, and significant additions are made to distributions and host ranges based on recently accumulated data.

Key to the North American Species of *Ceracis*

Males
(Abdominal sternite III with pubescent fovea)

1. Antennae 10-segmented 2
— Antennae with less than 10 segments 3
2. Elytral punctation distinctly seriate, the larger punctures forming relatively straight rows; pronotal apex bearing 2 horns, each with a rounded knob above it; abdominal

fovea slightly transverse; color of elytra usually reddish .... *C. singularis* (p. 502)
— Elytral punctation not distinctly seriate; pronotal apex with a raised, emarginate lamina; abdominal fovea circular; color of elytra usually black .... *C. magister* (p. 498)
3. Antennae 9-segmented 4
— Antennae 8-segmented 12
4. Pronotal apex rounded or shallowly emarginate, without distinct tubercles, horns, or lamina 5
— Pronotal apex produced, forming a lamina or 2 horns or tubercles 7
5. Frontoclypeal ridge produced, forming a long, narrow, median horn; pronotal and elytral punctation very fine and sparse; metasternal suture more than 0.20 × as long as median length of metasternum .... *C. monocerus* (p. 499)
— Frontyclypeal ridge simple or forming 2 rounded plates or tubercles; elytral punctation much coarser and denser than pronotal punctation; metasternal suture less than 0.20 × as long as median length of metasternum 6
6. Body longer and narrower, EL/EW more than 1.45; EL/PL more than 1.85; pronotal apex very shallowly emarginate; elytral punctation dual and confused; southern Arizona and western Mexico .... *C. powelli* (p. 501)
— Body shorter and broader, EL/EW less than 1.45; EL/PL less than 1.85; pronotal apex rounded; elytral punctation single and uniform; Florida and the West Indies .... *C. multipunctatus* (p. 499)
7. Elytral punctation single and uniform, very coarse and dense; EL/EW less than 1.35; surfaces of pronotum and elytra finely granulate or smooth and shiny 8
— Elytral punctation dual, the punctures falling into 2 size classes; if obscurely dual, then EL/EW more than 1.35 or pronotum coarsely granulate and dull in contrast to smooth and shiny elytra 9
8. Size larger, TL usually more than 1.55 mm; sides of elytra somewhat rounded; body somewhat shorter and broader; surfaces of pronotum and elytra smooth; pronotal apex bearing 2 approximate tubercles .... *C. curtus* (p. 497)
— Size smaller, TL usually less than 1.55 mm; sides of elytra subparallel; body somewhat longer and narrower; surfaces of pronotum and elytra finely granulate; pronotal apices bearing 2 widely-spaced tubercles .... *C. nigropunctatus* (p. 499)
9. Elytral punctation distinctly seriate, the larger punctures forming relatively straight rows; pronotal apex bearing 2 approximate, flattened horns with rounded apices .... *C. pullulus* (p. 501)
— Elytral punctation not distinctly seriate; pronotal armature different 10
10. Body shorter and broader, EL/EW less than 1.37; pronotal apex with a short, broad, elevated, shallowly emarginate lamina .... *C. pecki* (p. 499)
— Body longer and narrower, EL/EW more than 1.37; pronotal apex with a deeply emarginate lamina or 2 horns 11
11. Pronotal apex with a deeply emarginate lamina or 2 slightly tumid, subtriangular horns; elytral punctation coarser and denser, the punctures usually separated by less than 0.75 diameter; size somewhat larger, TL usually more than 1.50 mm; elytra somewhat longer and narrower, EL/EW usually more than 1.44; western North America .... *C. californicus* (p. 497)
— Pronotal apex with 2 distinctly tumid, narrow, diverging horns; elytral punctation finer and sparser, the punctures usually separated by more than 0.75 diameter; size somewhat smaller, TL usually less than 1.55 mm; elytra somewhat shorter and broader, EL/EW usually less than 1.48; eastern North America .... *C. thoracicornis* (p. 502)
12. Pronotal apex rounded or shallowly emarginate, without distinct horns, tubercles, or lamina; abdominal fovea strongly transverse and at least 0.50 × as long as body of sternite III 13
— Pronotal apex produced, forming a lamina or 2 horns or tubercles; abdominal fovea not or slightly transverse and less than 0.50 × as long as body of sternite III 14
13. Size larger, TL more than 1.40 mm; frontoclypeal ridge simple; pronotal disc strongly declined anteriorly, the apex rounded; elytra expanded apically .... *C. obrieni* (p. 499)
— Size smaller, TL less than 1.40 mm; frontoclypeal ridge forming 2 tubercles; pronotal disc only weakly declined, the apex shallowly emarginate; elytra subparallel .... *C. dixiensis* (p. 498)
14. Body longer and narrower, TL/EW more than 2.40; apex of pronotum with 2 narrowed, slightly diverging horns .... *C. quadricornis* (p. 501)
— Body shorter and broader, TL/EW less than 2.40; apex of pronotum with a short, broad lamina or 2 flattened, subtriangular horns 15
15. Elytral punctation much coarser and denser than pronotal punctation 16
— Elytral punctation as fine and sparse as or

finer and sparser than pronotal punctation 18

16. Size smaller, TL usually less than 1.30 mm; EL/PL usually more than 1.60; pronotal punctation somewhat finer and sparser, the punctures usually less than 0.10 × as large as scutellar base and separated by more than 1.5 diameters; pronotal apex with 2 approximate, triangular horns; color black or dark brown, with pronotal apex yellowish; eastern North America .... *C. minutissimus* (p. 499)

— Size larger, TL usually more than 1.30 mm; EL/PL usually less than 1.60; pronotal punctation somewhat coarser and denser, the punctures usually more than 0.10 × as large as scutellar base and separated by less than 1.5 diameters; pronotal apex with a short, broad, elevated lamina; color usually uniformly reddish; western North America and Mexico 17

17. Elytra shorter and broader, EL/EW usually less than 1.32; pronotal lamina shorter, broader, less abrupt, and strongly elevated at apex (Fig. 36); southern Texas and eastern Mexico .... *C. schaefferi* (p. 502)

— Elytra longer and narrower, EL/EW usually more than 1.32; pronotal lamina longer, narrower, more abrupt, and weakly elevated (Fig. 35); western Mexico and Baja California .... *C. similis* (p. 502)

18. Size smaller, TL less than 1.5 mm; abdominal fovea less than 0.33 × as long as body of sternite III; pronotal apex with 2 subparallel or slightly diverging, narrow horns; elytral punctation subseriate .... *C. minutus* (p. 499)

— Size larger, TL more than 1.5 mm; abdominal fovea more than 0.33 × as long as body of sternite III; pronotal apex with a deeply emarginate lamina, giving the appearance of 2 broad, subtriangular horns; elytral punctation confused 19

19. Pronotal punctation as fine and sparse as elytral punctation, the punctures usually separated by 1 diameter or more; abdominal fovea slightly transverse .... *C. sallei* (p. 501)

— Pronotal punctation somewhat coarser and denser than elytral punctation, the punctures usually separated by less than 1 diameter; abdominal fovea circular .... *C. punctulatus* (p. 501)

Females

(Abdominal sternite III simple)

1. Antennae 10-segmented 2

— Antennae with less than 10 segments 3

2. Elytral punctation distinctly seriate, the larger punctures forming relatively straight rows; color of elytra usually reddish; eastern North America, north of the Florida peninsula .... *C. singularis* (p. 502)

— Elytral punctation not distinctly seriate; color of elytra usually black; Florida Keys .... *C. magister* (p. 498)

3. Antennae 9-segmented 4

— Antennae 8-segmented 12

4. Elytral punctation single and confused, very coarse and dense, the punctures separated by 0.50 diameters or less; EL/EW less than 1.40 5

— Elytral punctation distinctly dual, the punctures falling into 2 size classes; if obscurely dual, EL/EW more than 1.40 7

5. Pronotal punctation finer and sparser, the punctures less than 0.10 × as large as scutellar base and separated by more than 0.75 diameter; pronotal disc strongly declined anteriorly, its surface distinctly granulate and dull, in contrast to the smooth and shiny elytral surface .... *C. multipunctatus* (p. 499)

— Pronotal punctation coarser and denser, the punctures more than 0.10 × as large as scutellar base and separated by less than 0.75 diameter; pronotal disc not or weakly declined anteriorly, its surface similar in texture to that of elytra 6

6. Size larger, TL usually more than 1.55 mm; sides of elytra somewhat rounded; pronotum shorter and broader, PL/PW usually less than 0.88; surfaces of pronotum and elytra smooth .... *C. curtus* (p. 497)

— Size smaller, TL usually less than 1.55 mm; sides of elytra subparallel; pronotum longer and narrower, PL/PW usually more than 0.88; surfaces of pronotum and elytra finely granulate .... *C. nigropunctatus* (p. 499)

7. Elytral punctation distinctly seriate, the larger punctures forming relatively straight rows; pronotal punctures separated by more than 1 diameter; southeastern U. S. and West Indies .... *C. pullulus* (p. 501)

— Elytral punctation not distinctly seriate; if subseriate, pronotal punctures separated by less than 1 diameter and distribution western 8

8. Elytral punctation finer and sparser, the punctures usually smaller than those on pronotum and separated by more than 1 diameter; EL/PL more than 1.50; eastern North America 9

— Elytral punctation coarser and denser, the megapunctures larger than pronotal punctures and separated by less than 1 diameter; EL/PL less than 1.50 or distribution western 10

9. Pronotal punctation very fine and sparse, the punctures less than 0.10 × as large as scutellar base and separated by 1.5 diameters or more; pronotum somewhat shorter and broader, PL/PW usually less than 0.91; metasternal suture more than 0.20 × as long as median length of metasternum; pronotum usually lighter in color than elytra .... *C. monocerus* (p. 499)
— Pronotal punctation coarser and denser, the punctures more than 0.10 × as large as scutellar base and separated by less than 1.5 diameters; pronotum somewhat longer and narrower, PL/PW usually more than 0.91; metasternal suture less than 0.20 × as long as median length of metasternum; pronotum and elytra similar in color or pronotum darker .... *C. thoracicornis* (p. 502)
10. Pronotum strongly declined anteriorly and relatively long, EL/PL less than 1.50; elytra shorter and broader, EL/EW less than 1.37; color usually reddish; southeastern U. S. .... *C. pecki* (p. 499)
— Pronotum not or weakly declined anteriorly and relatively shorter, EL/PL more than 1.50; elytra longer and narrower, EL/EW more than 1.37; color usually black or red and black; western North America 11
11. Pronotum distinctly narrowed anteriorly; EL/PL more than 1.85; antennal segment III 2.0 × as long as IV; size smaller, TL usually less than 1.52 mm .... *C. powelli* (p. 501)
— Pronotum not narrowed anteriorly; EL/PL less than 1.85; antennal segment III 3.0 × as long as IV; size larger, TL usually more than 1.45 mm .... *C. californicus* (p. 497)
12. Pronotal disc strongly declined anteriorly; elytra expanded apically; southern Arizona and northern Mexico .... *C. obrieni* (p. 499)
— Pronotal disc not or only weakly declined; elytra not expanded apically 13
13. TL/EW more than 2.35; elytral punctures separated by 0.75 diameter or more, not subconfluent anteriorly; southern Texas, eastern Mexico, and Central America .... *C. quadricornis* (p. 501)
— TL/EW less than 2.35 or elytral punctures separated by less than 0.75 diameter and becoming subconfluent anteriorly 14
14. Elytral punctation coarser and denser than that of pronotum, the elytral punctures becoming subconfluent anteriorly 15
— Elytral punctation finer and sparser than or as fine and sparse as that of pronotum, the elytral punctures not subconfluent anteriorly 8
15. Size smaller, TL usually less than 1.30 mm; EL/PL more than 1.60; color of elytra uniformly black 16
— Size larger, TL usually more than 1.30 mm; EL/PL less than 1.60; color of elytra reddish or black and red, rarely black 17
16. Pronotum somewhat shorter and broader, PL/PW usually less than 0.90; antennal segment III 1.50 × as long as IV; eastern North America .... *C. minutissimus* (p. 499)
— Pronotum somewhat longer and narrower, PL/PW usually more than 0.90; antennal segment III 2.0 × as long as IV; western North America .... *C. dixiensis* (p. 498)
17. Elytra shorter and broader, EL/EW usually less than 1.32; southern Texas and eastern Mexico .... *C. schaefferi* (p. 502)
— Elytra longer and narrower, EL/EW usually more than 1.32; western Mexico and Baja California .... *C. similis* (p. 502)
18. Size smaller, TL less than 1.10 mm; elytral punctation subseriate; pronotal surface lightly granulate and shiny .... *C. minutus* (p. 499)
— Size larger, TL usually more than 1.10 mm; elytral punctation confused; pronotal surface distinctly granulate and dull 19
19. Pronotal punctation about as fine and sparse as elytral punctation, the punctures usually separated by more than 1 diameter .... *C. sallei* (p. 501)
— Pronotal punctation coarser and denser than elytral punctation, the punctures usually separated by less than 1 diameter .... *C. punctulatus* (p. 501)

Ceracis californicus (Casey)

Ennearthron californicum Casey, 1884: 36.
Ceracis californicus (Casey),— Lawrence, 1967b: 107–110, figs. 15, 29. *See* Lawrence (1967b) for complete synonymy.

Distribution. See Lawrence (1967b). Also known from Rio Florido, 50 mi. from Parral, CHIHUAHUA.

Host fungi. See Lawrence (1967b).

Ceracis curtus (Mellié)

Ennearthron curtum Mellié, 1848: 367, pl. 12, fig. 15.
Ceracis curtis (Mellié), — Lawrence, 1967b: 110–112, fig. 30. *See* Lawrence (1967b) for complete synonymy.

Distribution. See Lawrence (1967b). Also known from Great Inagua, BAHAMAS; Isla de Pinos, CUBA; Dunedin,

Pinellas Co., FLORIDA; and Windsor, 10 mi. S Falmouth, Trelawny Par., JAMAICA.

Host fungi. Polyporus hydnoides [2(1)]; *Fomes sclerodermeus* [1].

Ceracis dixiensis (Tanner)

Octotemnus dixiensis Tanner, 1934: 47.
Ceracis dixiensis (Tanner), — Lawrence, 1967b: 112–113, fig. 33.

Distribution. See Lawrence (1967b). Also known from Rio Florido, 50 mi. from Parral, CHIHUAHUA.

Host fungi. Trametes hispida [10(8)]; *Ganoderma* sp. [1].

Ceracis magister NEW SPECIES

Holotype. ♂, FLORIDA: Lignum Vitae Key, Monroe Co., June 1, 1968, Lot 2600 J. F. Lawrence, ex *Fomes robiniae* [MCZ No. 31694]. Allotype, ♀, same data [MCZ].

Male. Length 1.80 mm. Body 2.18 × as long as broad. Head, pronotum, and elytra black, elytral suture somewhat reddish. Vertex with a deep, semicircular, transverse impression, preceded by a median elevation; frontoclypeal ridge produced and deeply emarginate, forming 2 triangular plates. Antennae 10-segmented; segment III 1.12 × as long as IV. Pronotum 0.93 × as long as broad, widest at posterior third, strongly declined anteriorly; sides weakly rounded; anterior edge produced forming a flat, elevated lamina which is deeply emarginate, giving an appearance of 2 somewhat rounded plates; disc impressed anteriorly just behind lamina and bearing a short, oblique carina on each side of it; surface distinctly granulate; punctures 0.17 × as large as scutellar base and separated by 1.50 to 2.0 diameters. Elytra 1.30 × as long as broad and 1.48 × as long as pronotum; sides subparallel, apices blunt; punctation dual and confused, much coarser and denser than pronotal punctation. Metasternum 0.48 × as long as wide; suture 0.15 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.25 × as long as body of sternite, distinctly margined, and located posterad of center.

Female. Length 1.77 mm. Body 2.15 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.96 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.30 × as long as broad and 1.54 × as long as pronotum. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to black, usually black, often somewhat reddish anteriorly. Elytra yellowish to black, usually black and somewhat reddish along suture. In smaller males the frontoclypeal tubercles are rounded and the pronotal lamina is shallowly emarginate, while in some larger specimens the pronotum bears two distinct, rounded plates which are slightly divergent. Size and dimensions vary as follows in a series of 21 males and 20 females from Lignum Vitae Key, Monroe Co., Florida (Lot 2600):

TL mm: ♂ 1.45–2.07 (1.74 ± 0.033), ♀ 1.55–1.92 (1.68 ± 0.023);
TL/EW: ♂ 2.14–2.32 (2.21 ± 0.010), ♀ 2.06–2.33 (2.17 ± 0.010);
PL/PW: ♂ 0.88–0.97 (0.94 ± 0.005), ♀ 0.86–0.97 (0.92 ± 0.007);
EL/EW: ♂ 1.29–1.38 (1.33 ± 0.005), ♀ 1.30–1.40 (1.34 ± 0.005);
EL/PL: ♂ 1.39–1.64 (1.50 ± 0.013), ♀ 1.50–1.75 (1.61 ± 0.015);
GD/EW: ♂ 0.87–0.97 (0.92 ± 0.005), ♀ 0.90–0.97 (0.93 ± 0.005).

Total size range in material examined: 1.45–2.25 mm.

Paratypes. FLORIDA: 2, Lignum Vitae Key, Monroe Co., May 27, 1968, Lot 2577 JFL, ex *Fomes robiniae* [JFL]; 48, same locality, June 1, 1968, Lot 2600 JFL, ex *Fomes robiniae* [FMNH, JFL, MCZ, USNM]; 4, same locality and date, Lot 2601 JFL, ex *Fomes robiniae* [JFL]; 11, same locality, June 5, 1968, Lot 2623 JFL, ex *Fomes robiniae* [JFL].

Distribution. Known only from Lignum Vitae Key, Florida.

Host fungi. Fomes robiniae [4(4)].

Discussion. This is one of the two North American *Ceracis* with 10-segmented antennae, and it is easily distinguished from the other, *C. singularis,* by the confused elytral punctation, darker color, and different male armature. It appears to be most closely related to *C. pecki,* from which it differs in antennal segmentation, color, and relative length of pronotum. *C. magister* and *C. pecki* belong to a group of Central American and West Indian species (all undescribed) that breed in melanic conks and are usually fairly large, with 9- or 10-segmented antennae and a short pronotal lamina in the male.

Ceracis magister is known only from the Florida Keys and may occur in the Greater Antilles. On Lignum Vitae Key, it breeds in the conks of *Fomes robiniae*, along with *Cis niedhauki, Malacocis brevicollis,* and *Ceracis punctulatus.*

Ceracis minutissimus (Mellié)

Cis minutissimus Mellié, 1848: 334, pl. 11, fig. 12.
Ceracis minutissimus (Mellié), — Lawrence, 1967b: 113–114, figs. 18, 32.

Distribution and host fungi. See Lawrence (1967b).

Ceracis minutus Dury

Ceracis minuta Dury, 1917: 25; Lawrence, 1967b: 114–115, figs. 19, 33.

Distribution. See Lawrence (1967b). Also known from the BAHAMAS; Lignum Vitae Key, Big Pine Key, Plantation Key, and Key Largo, Monroe Co., FLORIDA; Kingston, Windsor, Mt. Diablo, and Ewarton, JAMAICA.

Host fungi. Polyporus pinisitus [10(6)]; *Polyporus hydnoides* [7(4)]; *Stereum papyrinum* [5(3)]; *Polyporus maximus* [3(3)]; *Polyporus occidentalis* [3(3)]; *Polyporus sanguineus* [3(3)]; *Daedalea elegans* [1(1)]; *Trametes corrugata* [1(1)]; *Fomes sclerodermeus* [1].

Ceracis monocerus Lawrence

Ceracis monocerus Lawrence, 1967b: 115–116, figs. 20, 30. Replacement name for *Enncarthron unicorne* Casey, 1898: 90 (not *Ceracis unicornis* Gorham, 1898: 332).

Distribution and host fungi. See Lawrence (1967b).

Ceracis multipunctatus (Mellié)

Enncarthron multipunctatum Mellié, 1848: 368, pl. 12, fig. 16.
Ceracis multipunctatus (Mellié), — Lawrence 1967b: 116–118, figs. 24, 32.

Distribution. See Lawrence (1967b). Also known from Wakulla Springs State Park, Wakulla Co., FLORIDA; Adelphi, 3 mi. NW Ulster Spr., 10 mi. S Falmouth, and Ewarton, JAMAICA.

Host fungi. Ganoderma zonatum [6(5)]; *Fomes sclerodermeus* [4(4)]; *Ganoderma applanatum* [4(4)]; *Ganoderma lucidum* [1]; *Polyporus hydnoides* [1]; *Polyporus supinus* [1].

Ceracis nigropunctatus Lawrence

Ceracis nigropunctatus Lawrence, 1967b: 118–119, figs. 16, 27.

Distribution. See Lawrence (1967b). Also known from Antigua Morelos, TAMAULIPAS, and Madden Dam, CANAL ZONE.

Host fungi. Polyporus hydnoides [9(4)]; *Ganoderma* sp. [2]; *Polyporus hirsutus* [2]; *Fomes sclerodermeus* [1(1)].

Ceracis obrieni Lawrence

Ceracis obrieni Lawrence, 1967b: 119–120, figs. 25, 29.

Distribution. See Lawrence (1967b). Known also from Peña Blanca, Santa Cruz Co., ARIZONA.

Host fungi. See Lawrence (1967b).

Ceracis pecki NEW SPECIES

Holotype. ♂, FLORIDA: Florida Caverns State Park, Jackson Co., Sept. 6, 1968, Lot 2670 J. F. Lawrence (S. B. Peck, coll.)

ex *Poria nigra* [MCZ No. 31695]. Allotype, ♀, same data. [MCZ].

Male. Length 1.77 mm. Body 2.22 × as long as broad. Head and pronotum dark, reddish brown, elytra reddish. Vertex with a deep transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave, elevated lamina, which is shallowly emarginate at apex. Antennae 9-segmented; segment III 2.0 × as long as IV. Pronotum 0.97 × as long as broad, widest at middle; sides weakly rounded; anterior edge produced, forming a flat, slightly elevated lamina which is shallowly emarginate; disc impressed anteriorly just behind lamina and bearing a short oblique carina on each side of it; surface distinctly granulate; punctures 0.20 × as large as scutellar base and separated by 0.50–1.0 diameter. Elytra 1.28 × as long as broad and 1.37 × as long as pronotum; sides subparallel, apices blunt; punctation indistinctly dual and confused; punctures coarser and denser than those on pronotum. Metasternum 0.44 × as long as wide; suture 0.14 × as long as median length of sternum. Abdominal sternite III bearing a median, circular, pubescent fovea, which is 0.50 × as long as body of sternite, indistinctly margined and located about in center.

Female. Length 1.70 mm. Body 2.19 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 1.00 × as long as broad; anterior edge strongly rounded, simple. Elytra 1.29 × as long as broad and 1.43 × as long as pronotum. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to brown, usually reddish brown. Elytra yellowish to brown, usually reddish. Frontoclypeal and pronotal laminae in smaller males barely developed. Size and dimensions vary as follows in a series of 25 males and 25 females from Florida Caverns State Park, Jackson Co., Florida (Lot 2760):

TL mm: ♂ 1.47–2.02 (1.68 ± 0.028), ♀ 1.32–1.95 (1.66 ± 0.031);
TL/EW: ♂ 2.11–2.33 (2.20 ± 0.011), ♀ 2.12–2.25 (2.19 ± 0.007);
PL/PW: ♂ 0.93–1.03 (0.97 ± 0.005), ♀ 0.93–1.00 (0.98 ± 0.004);
EL/EW: ♂ 1.21–1.37 (1.28 ± 0.007), ♀ 1.23–1.32 (1.29 ± 0.005);
EL/PL: ♂ 1.25–1.50 (1.38 ± 0.021), ♀ 1.35–1.48 (1.42 ± 0.008);
GD/EW: ♂ 0.86–0.93 (0.90 ± 0.004), ♀ 0.86–0.94 (0.90 ± 0.004).

Total size range in material examined: 1.32–2.13 mm.

Paratypes. FLORIDA: 52, same data as holotype [FMNH, JFL, MCZ, USNM]; ILLINOIS: 1, Starved Rock State Park, LaSalle Co., X–24–1953, leaf mold, C. Ziolkowski leg. [FMNH]; MARYLAND: 1, Oakland, 10.7 [USNM]; VIRGINIA: 1, (no specific locality) [CIN].

Distribution. Eastern United States, from Illinois and Maryland south to Florida.

Host fungi. Poria nigra [1(1)].

Discussion. This species is characterized by the relatively large size, 9-segmented antennae, short and broad elytra with coarse and dense, obscurely dual, confused punctation, relatively elongate pronotum with fine, sparse punctation and coarsely granulate surface, reddish color, and short, broad pronotal lamina in the male. *C. magister* and *C. singularis* are similar, but the former is darker in color with a relatively shorter pronotum, the latter has distinctly seriate elytral punctation, and both have 10-segmented antennae. Other species with 9-segmented antennae have single elytral punctation (*C. curtus* and *C. nigropunctatus*), seriate elytral punctation (*C. pullulus*), finer and sparser elytral punctation (*C. monocerus* and *C. thoracicornis*) or longer and narrower elytra (*C. powelli* and *C. californicus*). Larger specimens of *C. sallei* resemble this species, but the antennae are 8-segmented, the pronotum is relatively shorter, and the male armature is different.

Ceracis pecki is known from a few scattered localities but may be distributed

throughout the Southeast. It appears to be most closely related to *C. magister* and to several undescribed forms from Central America. It has been taken only in *Poria nigra*, which is unusual in having a dark chocolate or violet-brown fruiting body.

Ceracis powelli Lawrence

Ceracis powelli Lawrence, 1967b: 120–121, figs. 23, 27.

Distribution and host fungi. See Lawrence (1967b).

Ceracis pullulus (Casey)

Ennearthron pullulum Casey, 1898: 90.
Ceracis pullulus (Casey), — Lawrence, 1967b: 121–123, figs. 22, 28.

Distribution. See Lawrence (1967b). Also known from Pine Mountain State Park, Harris Co., GEORGIA; Atlantic Beach, Carteret Co., NORTH CAROLINA; Cerro Doña Juana, Ponce, PUERTO RICO; West Union, Oconee Co., SOUTH CAROLINA; 1 mi. NW Adams, Robertson Co., TENNESSEE; and Cinnamon Bay, St. John, VIRGIN ISLANDS.

Host fungi. Polyporus gilvus [20(8)]; *Polyporus licnoides* [7(6)]; *Polyporus porrectus* ? [4(4)]; *Ganoderma zonatum* [4(2)]; *Polyporus iodinus* [2(1)]; *Polyporus hydnoides* [2]; *Polyporus corrosus* [1(1)]; *Poria nigra* [1(1)]; *Polyporus vinosus* [1].

Ceracis punctulatus Casey

Ceracis punctulata Casey, 1898: 90; Lawrence, 1967b: 123–124, fig. 34.
Ceracis punctulatus rubiculus Lawrence, 1967b: 124–127, figs. 13, 34.

Distribution. See Lawrence (1967b). Also known from Big Pine Key, Bill Find's Key, Crawl Key, Grassy Key, Key Largo, Lignum Vitae Key, Plantation Key, and Upper Matecumbe Key, Monroe Co., FLORIDA; and Windsor, 10 mi. S Falmouth, Trelawny Par., JAMAICA.

Host fungi. Polyporus gilvus [46(25)]; *Polyporus hydnoides* [18(9)]; *Fomes robiniae* [5(2)]; *Polyporus fulvocinereus* [3(2)]; *Ganoderma zonatum* [3(1)]; *Polyporus licnoides* [2(2)]; *Stereum papyrinum* [2(2)]; *Polyporus sanguineus* [2]; *Polyporus porrectus* ? [1(1)]; *Fomes fomentarius* [1]; *Ganoderma curtisii* [1]; *Ganoderma lucidum* [1]; *Ganoderma* sp. [1]; *Polyporus adustus* [1]; *Polyporus pargamenus* [1]; *Polyporus pinisitus* [1]; *Stereum ostrea* [1]; *Trametes corrugata* [1].

Discussion. A large series of specimens collected in the Florida Keys shows a great deal of variation in size and color, and individuals are, on the average, smaller and more reddish than those from central and southern Florida. These island populations seem to prefer a wider variety of fungi and were found breeding on *Polyporus fulvocinereus* and *Stereum papyrinum*, as well as *Polyporus hydnoides* and *Fomes robiniae*. The species appears to be common in the area and is the only ciid collected on Bill Find's Key, a small red mangrove island near Sugarloaf Key.

Ceracis quadricornis Gorham

Ceracis quadricornis Gorham, 1886: 359; Lawrence, 1967b: 127–128, figs. 17, 30.

Distribution. See Lawrence (1967b). Also known from Chorros de Agua, 13 mi. W Montemorelos, NUEVO LEÓN; and Antiguo Morelos, TAMAULIPAS.

Host fungi. Polyporus occidentalis [7(4)]; *Polyporus hydnoides* [5(4)]; *Polyporus maximus* [4(3)]; *Polyporus hirsutus* [2(1)]; *Trametes corrugata* [1(1)]; *Polyporus crocatus* [1]; *Trametes cirrifer* [1].

Ceracis sallei Mellié

Ennearthron (Ceracis) sallei Mellié, 1848: 377, pl. 12, fig. 22.
Ceracis sallei Mellié, — Lawrence, 1967b: 128–130, fig. 11, 26.

Distribution. See Lawrence (1967b).

Host fungi. Ganoderma applanatum [31(16)]; *Ganoderma curtisii* [3(1)]; *Ganoderma zonatum* [2(1)]; *Polyporus hydnoides* [2(1)]; *Fomes connatus* [1(1)]; *Ganoderma lobatum* [1(1)]; *Fomes pini-*

cola [1]; *Fomes sclerodermeus* [1]; *Ganoderma* sp. [1]; *Polyporus cinnabarinus* [1].

Ceracis schaefferi Dury

Ceracis schaefferi Dury, 1917: 25; Lawrence, 1967b: 130–131, figs. 14, 28.

Distribution and host fungi. See Lawrence (1967b).

Ceracis similis Horn

Ceracis similis Horn, 1894: 391; Casey, 1898: 90; Dury, 1917: 27. Type locality: "Coral de Piedra, Sierra el Taste" [Baja California]. Types, CAS.

Distribution. Baja California Sur and Nayarit south to El Salvador. Marginal records: Porto Balandra, Carmen Is.; San José del Cabo, BAJA CALIFORNIA SUR; San Blas, NAYARIT; 45 mi. N Acatlán, PUEBLA; 2 mi. S Quezaltepeque, EL SALVADOR.

Host fungi. Ganoderma zonatum [3(3)]; *Ganoderma* sp. [2(2)]; *Ganoderma applanatum* [1(1)].

Discussion. Although this species has not been recorded from the United States, it is included here because of its occurrence on several of the islands in the Gulf of California. It is possible that further collecting in extreme southern California may reveal the presence of *C. similis* there. The species most closely resembles *C. schaefferi* from eastern Mexico and southern Texas.

Ceracis singularis (Dury)

Xestocis singularis Dury, 1917: 14.
Ceracis singularis (Dury), — Lawrence, 1967b: 131–132, figs. 12, 33.

Distribution. See Lawrence (1967b). Also known from Chattahoochie State Park, Houston Co., ALABAMA; Florida Caverns State Park, Jackson Co., FLORIDA; Spring Mill State Park, Lawrence Co., INDIANA; Wildcat Den State Park, Muscatine Co., IOWA; and Madison, Dane Co., WISCONSIN.

Host fungi. Polyporus gilvus [12(7)]; *Ganoderma applanatum* [8(2)]; *Fomes robiniae* [4(1)]; *Fomes igniarius* [2(1)]; *Ganoderma curtisii* [2(1)]; *Poria nigra* [2(1)]; *Fomes sclerodermeus* [2]; *Polyporus pargamenus* [2]; *Fomes ribis* [1(1)]; *Lenzites saepiaria* [1(1)]; *Daedalea confragosa* [1]; *Fomes annosus* [1]; *Ganoderma* sp. [1]; *Ganoderma tsugae* [1]; *Polyporus licnoides* [1]; *Polyporus supinus* [1]; *Polyporus versicolor* [1]; *Trametes hispida* [1]; *Trametes plebeja* [1].

Ceracis thoracicornis (Ziegler)

Cis thoracicornis Ziegler, 1845: 270.
Ceracis thoracicornis (Ziegler), — Lawrence, 1967b: 132–136, figs. 21, 31. *See* Lawrence (1967b) for complete synonymy.

Distribution. See Lawrence (1967b). Numerous additional records have made no significant changes in the range.

Host fungi. Polyporus pargamenus [41(15)]; *Polyporus supinus* [25(15)]; *Polyporus adustus* [15(6)]; *Polyporus versicolor* [11(3)]; *Lenzites betulina* [10(6)]; *Daedalea ambigua* [9(7)]; *Ganoderma applanatum* [7]; *Polyporus sector* [6(2)]; *Daedalea unicolor* [6(2)]; *Fomes ulmarius* [6(1)]; *Ganoderma lucidum* [5(2)]; *Ganoderma tsugae* [5(1)]; *Polyporus hirsutus* [4(1)]; *Polyporus squamosus* [3(2)]; *Polyporus abietinus* [3(1)]; *Polyporus gilvus* [3]; *Fomes sclerodermeus* [2(1)]; *Trametes corrugata* [2(1)]; *Stereum ostrea* [2]; *Trametes plebeja* [2]; *Ganoderma* sp. [1(1)]; *Polyporus spraguei* [1(1)]; *Polyporus tulipiferae* [1(1)]; *Poria vitrea* [1(1)]; *Trametes hispida* [1(1)]; *Trametes trogii* [1(1)]; *Boletus* sp. [1]; *Daedalea elegans* [1]; *Fomes fomentarius* [1]; *Fomes fraxineus* [1]; *Fomes pinicola* [1]; *Ganoderma curtisii* [1]; *Polyporus cinnabarinus* [1]; *Polyporus dichrous* [1]; *Polyporus hydnoides* [1]; *Polyporus sulphureus* [1]; *Polyporus vinosus* [1].

Genus *Sulcacis* Dury

Sulcacis Dury, 1917: 20; Lawrence, 1965: 278 (complete synonymy); Lohse, 1967: 284. Type species, by subsequent designation, *Sulcacis lengi* Dury, 1917: 21 (Lawrence, 1965: 278).

Entypus Redtenbacher, 1847: 350 (not Dahlbom, 1843: 35). Type species, by monotypy, *Cis affinis* Gyllenhal, 1827: 628 (misidentified as *Apate fronticornis* Panzer).
Entypus (*Entypocis*) Lohse, 1964: 121. Type species, by original designation, *Cis bidentulus* Rosenhauer, 1847: 58.
Sulcacis (*Entypocis*) Lohse, — Lohse, 1967: 284.

Included species. Cis affinis Gyllenhal, 1827: 628 [Eurasia]; *Cis bidentulus* Rosenhauer, 1847: 58 [southern Europe, northern Africa]; *Cis curtulus* Casey [northern North America, *see* p. 503]; *Apate fronticornis* Panzer, 1809: 98: 7 [Eurasia]; *Rhopalodontus japonicus* Nobuchi, 1960: 39 [Japan]; *Sulcacis lengi* Dury [eastern North America, *see* p. 504]. Total: 6 species.

Excluded species. Cis bicornis Rosenhauer (*see* p. 488); *Rhopalodontus tokunagai* Nobuchi (*see* p. 488).

This genus was discussed in detail by Lohse (1964, under *Entypus* and *Entypocis*) and Lawrence (1965), but the concept is somewhat modified in the present treatment by the transfer of *C. bicornis* and *R. tokunagai* to *Strigocis* (*see* p. 488). Species of *Sulcacis* may be distinguished from most other North American ciids by the spinose protibial apices, biconcave prosternum with a relatively broad, tapering intercoxal process, rounded anterior pronotal angles, and indistinctly dual vestiture, consisting of longer and shorter bristles. The most closely related group is *Malacocis*, in which the body form is shorter and broader and the prosternum very short and straplike.

Key to the North American Species of *Sulcacis*

1. Antennae 9-segmented; elytral punctation finer, punctures usually less than 0.20 × as large as scutellar base; pronotal surface dull; male with frontoclypeal ridge simple and abdominal fovea transversely oval .... *S. lengi* (p. 504)
— Antennae 10-segmented; elytral punctation coarser, punctures usually more than 0.20 × as large as scutellar base; pronotal surface somewhat shiny; male with frontoclypeal ridge bidentate and abdominal fovea circular .... *S. curtulus* (p. 503)

Sulcacis curtulus (Casey), NEW COMBINATION

Cis curtula Casey, 1898: 83; Weiss and West, 1920: 8 (dist., biol.); Lawrence, 1965: 277. Type locality: "New York." Holotype, ♂, Casey Coll., USNM.
Cis montana Casey, 1898: 82. Type locality: "Montana (Missoula)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.
Cis sorror Casey, 1898: 83; Hatch, 1962: 230, pl. 48, fig. 3, 3a (dist., biol.). Type locality: [Victoria] "Vancouver Island . . . " [British Columbia]. Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.
Cis cylindricus Dury, 1917: 8; Weiss, 1920a: 110–111 (biol.); Weiss and West, 1920: 8 (biol.); Weiss and West, 1921a: 61 (dist., biol.); Weiss and West, 1921b: 169 (dist., biol.); Hatch, 1962: 230 (syn. with *sorror*). Type locality: "Umatilla Co., Oregon." Syntypes, Dury Coll., CIN. NEW SYNONYMY.
Sulcacis niger Dury, 1917: 21. Type locality: "Southern Illinois." Holotype, ♀, Dury Coll., CIN. NEW SYNONYMY.
Cis criddlei Dury, 1919: 158. Type locality: "Aweme, Manitoba." Holotype, ♂, Dury Coll., CIN. NEW SYNONYMY.
Cis hystriculus Casey, — Weiss and West, 1921a: 61 (biol.). Misidentification.

Distribution. Widespread throughout the northern and montane regions of North America, from the northern coast of British Columbia to southern Quebec and New England, south to San Diego County, California, the mountains of southern Arizona and northern Mexico, and the states of Nebraska, Illinois, and North Carolina (Fig. 110). Marginal records: BRITISH COLUMBIA: Terrace. ALBERTA: McMurray. MANITOBA: Aweme. QUEBEC: Chelsea. NEW HAMPSHIRE: Intervale, Mt. Surprise, Carroll Co. NORTH CAROLINA: Southern Pines, Moore Co. ILLINOIS: Cahokia, St. Clair Co. NEBRASKA: Central City, Merrick Co.; 15 mi. W Sydney, Cheyenne Co. COLORADO: Pueblo, Pueblo Co. NEW MEXICO: (no specific locality). CHIHUAHUA: Rio Florido, 50 mi. from Parral. ARIZONA: Miller Canyon, 10 mi. W Hereford, Huachuca Mts., Cochise Co. CALIFORNIA: 10 mi. N Descanso, San Diego Co.

Host fungi. Polyporus versicolor [69

(35)]; *Polyporus hirsutus* [12(6)]; *Polyporus adustus* [11(3)]; *Lenzites betulina* [8(5)]; *Trametes hispida* [6(4)]; *Pleurotus ostreatus* [3]; *Polyporus cinnabarinus* [2(1)]; *Fomes igniarius* [2]; *Schizophyllum commune* [1(1)]; *Ganoderma applanatum* [1]; *Polyporus gilvus* [1]; *Polyporus vulpinus* [1]; *Steccherinum ochraceum* [1]; *Stereum hirsutum* [1].

Discussion. This species is similar in general form and punctation to *Dolichocis manitoba*, which is more elongate (EL/EW more than 1.50), with 9-segmented antennae, narrowly rounded protibial apex, and a fovea on the vertex in the male. *Sulcacis lengi* is somewhat shorter and broader and differs in having 9-segmented antennae and finer punctation. *Cis hystriculus* resembles *S. curtulus* in several respects, but differs in having the protibial apex dentate, the body more elongate, the pronotal punctation denser, the elytral bristles colorless (rather than yellow), and the abdominal fovea absent in the male. It appears to be most closely related to the Palaearctic *Sulcacis bidentulus* (Rosenhauer).

Sulcacis curtulus breeds in a number of fungi but prefers *Polyporus versicolor* and its relatives, as do other *Sulcacis* whose feeding habits have been recorded. Although the species is absent from the southwestern deserts, it is fairly widespread throughout the western mountains and along the Pacific Coast, frequenting both dry and humid habitats. Along the coast of California, it breeds in the conks of *Polyporus versicolor* and related fungi, in association with *Cis fuscipes*, *Cis vitulus*, *Cis versicolor*, and *Octotemnus laevis*. In the drier parts of the western mountains and at higher elevations, *S. curtulus* is often found alone in the same habitats. The species is much less common in eastern North America, although it is known from widely scattered localities.

Sulcacis lengi Dury

Sulcacis lengi Dury, 1917: 21; Weiss 1919b: 203–204 (biol.); Weiss and West, 1920: 8 (dist., biol.); Lawrence, 1965: 277. Type locality: "Vermont" [Bennington Co.]. Syntypes, Dury Coll., CIN.

Distribution. Eastern North America, from Maine to the Carolinas and west to eastern Kansas and Texas (Fig. 99). Marginal records: MAINE: Weld, Franklin Co.; NORTH CAROLINA: Calypso, Duplin Co.; SOUTH CAROLINA: Mountain Rest, Oconee Co.; MISSISSIPPI: 4 mi. W Starkville, Oktibbeha Co.; TEXAS: Huntsville, Walker Co.; KANSAS: Salina, Saline Co.; IOWA: Estherville, Emmet Co.; MICHIGAN: (no specific locality).

Host fungi. Polyporus versicolor [11(3)]; *Lenzites betulina* [5(2)]; *Polyporus pubescens* [1(1)]; *Polyporus hirsutus* [1]; *Boletus* sp. [1].

Discussion. This species is similar to *Malacocis brevicollis* in punctation, vestiture, protibial apices, and secondary sexual characters, and it may represent a link between *Sulcacis* and *Malacocis*. Members of the genus *Malacocis*, however, are characterized by the shorter and broader body form, and shortened pronotum, prosternum, and metasternum; in addition, *M. brevicollis* has 10-segmented antennae. *S. curtulus* differs in being more elongate and coarsely punctate, with 10-segmented antennae and different secondary sexual characters.

Sulcacis lengi occurs throughout the eastern part of the continent and breeds in the fruiting bodies of *Polyporus versicolor* and its relatives, in association with *Cis fuscipes*, *Strigocis opacicollis*, *Octotemnus laevis*, and several other ciid species.

Genus *Malacocis* Gorham

Malacocis Gorham, 1886: 356. Type species, by monotypy, *Malacocis championi* Gorham, 1883: 356.

Brachycis Casey, 1898: 86; Dury, 1917: 21; Leng, 1920: 247; Arnett, 1962: 829. Type species, by monotypy, *Brachycis brevicollis* Casey, 1898: 87. NEW SYNONYMY.

Included species. Brachycis brevicollis Casey [eastern North America, *see* p. 505];

Malacocis championi Gorham, 1883: 356 [Guatemala]. Total: 2 species.

Excluded species. Malacocis bahiensis Pic, 1916: 6 [Brazil]. *See* discussion below.

The genus *Malacocis* includes two described and several undescribed species from North and Central America and the West Indies. They are all characterized by the very short and broad body form, vestiture of short to moderately long bristles, straplike prosternum with tapering intercoxal process (Fig. 27), and spinose protibial apex (Fig. 57). The antennae are 10-segmented in the North American *M. brevicollis,* but in the Central American *M. championi* they are 9-segmented, and in an undescribed Mexican form there are only 8 segments. In the male, the pronotal apex is always simple and the frontoclypeal region usually bears two small teeth or tubercles. Some species of *Ceracis* are similar, but the prosternal intercoxal process is laminate and the vestiture consists of very short, fine hairs. The most closely related genus appears to be *Sulcacis*, in which the form is more elongate and the prosternum longer in front of the coxae.

Since Casey's species *Brachycis brevicollis* differs from *M. championi* in little more than antennal segmentation, which has undergone reduction in several groups of Ciidae, I have synonymized the junior name *Brachycis* above. Pic's species *Malacocis bahiensis* does not belong in this group at all, but rather is a member of the *Cis taurus* group (= *Macrocis* Reitter, *see* p. 439).

Malacocis brevicollis (Casey), NEW COMBINATION

Brachycis brevicollis Casey, 1898: 87; Dury, 1917: 21 (dist.); Gibson, 1918: 113 (dist.); Weiss, 1919a: 145–147 (biol.); Weiss and West, 1920: 8 (dist., biol.). Type locality: "New York (Ithaca)." Holotype, ♀, Casey Coll., USNM.

Distribution. Eastern North America, from northern Maine to the Florida Keys and west to southern Manitoba, eastern Kansas, and Texas (Fig. 108). Marginal records: MAINE: Baxter State Park, Piscataquis Co. QUEBEC: Montreal; Knowlton. FLORIDA: Lignum Vitae Key, Monroe Co. TEXAS: Austin, Travis Co. OKLAHOMA: South of Broken Bow, McCurtain Co. KANSAS: 5 mi. S Lawrence, Douglas Co. MANITOBA: Aweme. ONTARIO: 10 mi. SE Upsala.

Host fungi. Polyporus gilvus [36(16)]; *Fomes igniarius* [13(8)]; *Fomes robiniae* [6(3)]; *Fomes robustus* [4(2)]; *Fomes pomaceus* [3(2)]; *Polyporus licnoides* [3]; *Fomes everhartii* [2(1)]; *Fomes pini* [1(1)]; *Polyporus corrosus* [1(1)]; *Fomes fomentarius* [1]; *Fomes johnsonianus* [1]; *Polyporus hydnoides* [1]; *Polyporus vinosus* [1]; *Poria ferruginosa* [1]; *Poria laevigata* [1].

Discussion. Malacocis brevicollis is easily distinguished by the very short and broad body form, the short and straplike prosternum, shortened metasternum, spinose protibial apices, vestiture of short, stout, bristles, and lack of sexual ornaments on the clypeus or pronotum of the male. *Sulcacis lengi* is somewhat more elongate, with the prosternum and metasternum less reduced. In addition, *M. brevicollis* is usually larger in size and the elytra are usually brownish with reddish yellow bristles, while the smaller *S. lengi* has blackish elytra with yellow bristles. Another unique character in *M. brevicollis* is the tendency for the elytral punctures to become transversely confluent on the anteromesal part of the disc, so that a series of indistinct transverse ridges is formed.

There is considerable variation in color and vestiture within this species. Most nonteneral specimens are brownish and many have reddish brown elytra with black or dark brown prothorax. The bristles are shorter in specimens from northern populations, while those from the Southwest have longer bristles that fall into two size classes. One population from Key Largo is comprised entirely of small individuals that are darker in color and have shorter and more yellowish bristles than those of

other southern populations. This may well be a distinct species, but it is not treated as such here. The genus *Malacocis* contains a number of forms (mostly undescribed) from the West Indies, Mexico, and Central America, which should be studied as a unit before any more new species are described.

Malacocis brevicollis is probably the most common and characteristic North American inhabitant of the orange-brown conks characteristic of *Fomes robinae, F. igniarius, Polyporus gilvus* and other fungi usually included in the genera *Phellinus* and *Inonotus.* It may be associated with *Ceracis singularis, Ceracis punctulatus,* or *Ceracis pullulus,* as well as the tenebrionid *Platydema ellipticum* (Fabricius), but it usually occurs alone in the northern part of the range and in the larger, woodier conks.

Subfamily Orophiinae

Orophiina Thomson, 1863: 195.
Orophyidae Kiesenwetter, 1877: 194.
Octotemnidae Reitter, 1878b: 21.
Apatini (in part), — Seidlitz, 1872: 90 (in family Anobiidae).

Included genera. Octotemnus Mellié, *Paratrichapus* Scott, *Rhopalodontus* Mellié, *Scolytocis* Blair, and *Xylographus* Mellié.

Genus *Rhopalodontus* Mellié

Ropalodontus Mellié, 1847: 109; Mellié, 1848: 233. Type species by monotypy, *Cis perforatus* Gyllenhal, 1813: 385.
Rhopalodontus Mellié, — Gaubil, 1849: 123; Lacordaire, 1857: 550; Thomson, 1863: 195; Abeille de Perrin, 1874b: 76; Kiesenwetter, 1877: 194; Reitter, 1902a: 57; Dalla Torre, 1911: 21; Winkler, 1927: 794; Lohse, 1964: 117; Lawrence, 1965: 275; Lohse, 1967: 283; Lohse, 1969: 48–52. Justifiable emendation.
Rhopalodontus (*Cedrinus*) Abeille de Perrin, 1876: 312. Type species, by monotypy, *Rhopalodontus* (*Cedrinus*) *camelus* Abeille de Perrin, 1876: 312.
Cedrinus Abeille de Perrin, — Winkler, 1927: 791.
Cis Latreille, — Gyllenhal, 1813: 385.

Included species. Rhopalodontus americanus Lawrence, n. sp. [Wisconsin, *see* p. 507]; *R. armifrons* Reitter, 1913: 655 [Algeria]; *R. baudueri* Abeille de Perrin, 1874a: 52 [southern Europe]; *R. camelus* Abeille de Perrin, 1876: 312 [Lebanon]; *R. harmandi* Lesne, 1917: 191 [Japan]; *R. novorossicus* Reitter, 1902a: 58 [southeastern Europe]; *Cis perforatus* Gyllenhal, 1813: 385 [Eurasia]; *R. perrini* Reitter, 1878d: 221 [southeastern Europe]; *R. populi* Brisout de Barneville, 1877: cvii [southern Europe]; *R. strandi* Lohse, 1969: 50 [Scandinavia]. Total: 10 species.

Doubtfully included species. Rhopalodontus gyllenhali Gistel, 1857: 59 [Europe]; *R. sassaparillae* Motschulsky, 1852: 22 [Europe]. *See* discussion below.

Excluded species. Rhopalodontus japonicus Nobuchi (*see* p. 503); *R. tokunagai* Nobuchi (*see* p. 488).

Members of this genus may be distinguished from species of *Octotemnus* by the 10-segmented antennae, spinose protibial apices (Fig. 59), and vestiture of moderately long and fine, erect hairs. The male abdominal fovea in *Rhopalodontus* is covered (Fig. 31), as it is in *Octotemnus,* and this condition separates the two genera from *Xylographus, Scolytocis,* and *Paratrichapus.* In *Scolytocis* the antennae are 9-segmented, with a more compact club, while in *Paratrichapus* the tarsi have three segments (instead of four). The species of *Xylographus* are usually distinguished from those of *Rhopalodontus* by the form of the tibiae, which are spinose along the outer edge; this character may break down, however, in certain Indo-Pacific species. The male sexual ornaments in this genus are not spectacular and usually consist of tubercles on the frontoclypeal ridge and occasionally the pronotal apex.

Rhopalodontus gyllenhali and *R. sassaparillae* are doubtfully included in this genus, since types have not been seen and descriptions are completely inadequate. Neither name has been used since, and both probably should be rejected altogether. *Rhopalodontus japonicus* and *R.*

tokunagai have been transferred to *Sulcacis* and *Strigocis*, respectively (*see* p. 503 and 488).

Species of *Rhopalodontus* occur throughout Eurasia from Scandinavia to northern Africa, Burma, and Thailand (undescribed forms), and a single species has recently been discovered in North America (*see* below).

Rhopalodontus americanus NEW SPECIES

Holotype. ♂, WISCONSIN: Woodruff, Oneida Co., July 26, 1968, C. H. Porter, No. 68–57, ex *Polyporus betulinus* [FMNH]. Allotype, ♀, same data [FMNH].

Male. Length 1.82 mm. Body 2.21 × as long as broad, strongly convex. Head and pronotum reddish orange, elytra yellowish orange (teneral). Vestiture consisting of long, fine, erect, yellowish hairs. Vertex slightly concave with a low, median elevation; frontoclypeal ridge bearing 2 rounded tubercles which are separated by 2.0 basal widths. Antennal segment III 1.40 × as long as IV. Pronotum 0.83 × as long as broad, widest at posterior third; anterior edge strongly rounded, slightly flattened at middle; sides strongly rounded, the margins very narrow and weakly crenulate, not visible from above; anterior angles not produced, rounded; disc strongly convex, even; surface finely granulate and shiny; punctures 0.20 × as large as scutellar base and separated by 0.50 to 1.0 diameter. Elytra 1.45 × as long as broad and 1.92 × as long as pronotum; sides subparallel, apices blunt; punctation single and confused; punctures coarser and denser than those on pronotum, about 0.30 × as large as scutellar base and separated by 0.20 to 0.50 diameter, each puncture bearing a fine, erect, yellowish hair, which is about 1.25 × as long as scutellar base. Prosternum (Fig. 25) short and concave, 0.33 × as long as a procoxal cavity; intercoxal process short and subtriangular. Protibia with outer apical angle produced, rounded, and bearing 9 stout spines (Fig. 59). Metasternum 0.46 × as long as wide; strongly convex, flattened in middle; suture absent. Abdominal sternite III bearing a median, transversely oval, pubescent fovea, which is partly covered by a posteriorly projecting, subtriangular flap (Fig. 31).

Female. Length 1.97 mm. Body 2.19 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.82 × as long as broad; anterior edge strongly rounded. Elytra 1.44 × as long as broad and 1.93 × as long as pronotum. Sternite III without a pubescent fovea.

Variation. Pronotum yellowish orange to reddish brown, usually reddish brown. Elytra yellowish to reddish brown, usually reddish brown. Frontoclypeal tubercles in some males subacute. Anterior edge of pronotum in large males slightly emarginate at middle. Size and dimensions vary as follows in a series of 13 males and 13 females:

TL mm: ♂ 1.65–2.05 (1.84 ± 0.030), ♀ 1.75–1.97 (1.87 ± 0.022);
TL/EW: ♂ 2.00–2.21 (2.12 ± 0.017), ♀ 2.11–2.26 (2.15 ± 0.011);
PL/PW: ♂ 0.77–0.85 (0.81 ± 0.008), ♀ 0.81–0.87 (0.83 ± 0.005);
EL/EW: ♂ 1.32–1.47 (1.39 ± 0.012), ♀ 1.36–1.51 (1.42 ± 0.010);
EL/PL: ♂ 1.78–2.00 (1.90 ± 0.016), ♀ 1.81–2.04 (1.93 ± 0.019);
GD/EW: ♂ 0.85–0.93 (0.88 ± 0.006), ♀ 0.85–0.92 (0.89 ± 0.006).

Paratypes. WISCONSIN: 26, Woodruff, Oneida Co., July 26, 1968, C. H. Porter, No. 68–57, ex *Polyporus betulinus* [JFL, MCZ, USNM, UWS]; 5, same locality and date, C. H. Porter, No. 68–59, ex *Russula* sp. [JFL, UWS]; 5, Vilas Co. (no specific locality), July 26, 1968, C. H. Porter, No. 68–80, ex *Polyporus fibrillosus* [UWS]; 5, same locality and date, C. H. Porter, No. 68–83, ex *Fomes* sp. [JFL, UWS].

Distribution. Known only from northern Wisconsin.

Host fungi. Polyporus betulinus [1(1)];

Polyporus fibrillosus [1]; *Fomes* sp. [1]; *Russula* sp. [1].

Discussion. This species may be distinguished from all other North American Ciidae by the characters given in the generic key. It is similar to *Sulcacis curtulus* in general form, punctation, antennal segmentation, and protibial structure, but in that species the vestiture consists of shorter and stouter bristles, the prosternal intercoxal process is much longer, and the abdominal fovea in the male is not covered by a subtriangular flap. *R. americanus* is apparently related to the Palaearctic species *R. perforatus* (Gyllenhal), *R. novorossicus* Reitter, and *R. strandi* Lohse. It differs from *R. perforatus* in being more elongate (TL/EW more than 2.00), and having a shorter and broader prosternal intercoxal process. It may be distinguished from *R. novorossicus* by the longer hairs, coarser elytral punctation, and relatively simple pronotal apex. *R. americanus* closely resembles *R. strandi,* which was described from Scandinavia, but differs from the latter in being smaller and relatively shorter and broader, according to Lohse (*in litt.*), who has examined specimens of both species. According to Lohse's description, *R. strandi* is 1.7 to 2.2 mm long and 2.35 × as long as broad (*see* figures for *R. americanus* above). The aedeagus in *R. americanus* is similar to that of *R. strandi* (Lohse, 1969: 50, fig. 2b), except that the median lobe is slightly longer than the tegmen.

Although this new American species is known only from northern Wisconsin, it may be more widespread in the Boreal parts of the continent, where it may breed in *Polyporus betulinus* and perhaps *Fomes fomentarius*, both of which are common on birch. Host records are not available for *R. strandi*, but *R. perforatus* has been reported from *Fomes fomentarius* and *Polyporus betulinus* in Scotland (Paviour-Smith, 1969) and from *F. fomentarius* in Scandinavia (Saalas, 1923: Palm, 1959).

Genus *Octotemnus* Mellié

Octotemnus Mellié, 1847: 110; Mellié, 1848: 384; Lacordaire, 1857: 554; Jacquelin du Val, 1861: 239; Abeille de Perrin, 1874b: 90; Casey, 1898: 91; Reitter, 1902a: 60; Dalla Torre, 1911: 26; Dury, 1917: 28; Leng, 1920: 247; Arnett, 1962: 830. Type species, by subsequent designation, *Cis glabriculus* Gyllenhal, 1827: 627 (Jacquelin du Val, 1861: 239).

Orophyus (*Octotemnus*) Mellié, — Kiesenwetter, 1877: 197.

Orophyus Redtenbacher, 1847: 350; Lacordaire, 1857: 553; Thomson, 1863: 196; Dalla Torre, 1911: 26. Type species, by monotypy, *Cis mandibularis* Gyllenhal, 1813: 717.

Octotemnus (*Orophius*) Redtenbacher, — Reitter, 1878a: 21; Reitter, 1902a: 61.

Orophyus Kiesenwetter, 1877: 195. Incorrect subsequent spelling.

Orophinus Marschall, 1873: 226. Incorrect subsequent spelling.

Cis Latreille (in part), — Gyllenhal, 1813: 717; Gyllenhal, 1827: 627.

Included species. Orophius dilutipes Blackburn, 1891: 308 [Australia]; *Orophius diabolicus* Pic, 1916: 6 [India]; *Cis glabriculus* Gyllenhal, 1827: 629 [Eurasia]; *Orophius hebridarum* Blair, 1941: 178 [New Hebrides]; *Octotemnus* (*Orophius*) *japonicus* Miyatake, 1954: 64 [Japan]; *Octotemnus laevis Casey* [North America, *see* p. 509]; *Orophius laminifrons* Motschulsky, 1860: 17 [Japan]; *Cis mandibularis* Gyllenhal, 1813: 717 [Eurasia]; *Octotemnus mindanaonus* Chujo, 1966: 530 [Philippines]; *Octotemnus omogensis* Miyatake, 1954: 61 [Japan]; *Octotemnus opacus* Mellié, 1848: 386 [Madeira]; *Octotemnus palawanus* Chujo, 1966: 531 [Philippines]; *Octotemnus parvulus* Miyatake, 1954: 62 [Japan]; *Octotemnus* (*Orophius*) *punctidorsum* Miyatake, 1954: 63 [Japan]; *Orophius quadridentatus* Pic, 1916: 6 [Indo-China]; *Orophius testaceus* Pic, 1916: 6 [India]; *Octotemnus walkeri* Blair, 1940: 136 [Australia]. Total: 17 species.

This is a well-defined group of Orophiinae in which the antennae are 8-segmented, the tibiae spinose along most of the outer edge (Fig. 60), and the abdominal fovea in the male is covered by a flap (Fig. 31).

In *Xylographus* and *Scolytocis* the tibiae are similar, but the antennae are 10- or 9-segmented and the abdominal fovea is naked or absent. In *Rhopalodontus* and *Paratrichapus,* the tibiae are spinose at the apices only and the antennae are 10-segmented. Most species of *Octotemnus* are subglabrous with a few scattered, erect hairs; the Madeiran species, *O. opacus,* however, has the entire surface covered with fine, decumbent, but easily visible hairs. Secondary sexual characters in the genus are unique in that males of several species have enlarged mandibles resembling those of stag beetles (Lucanidae). Males of some species have lateral setiferous tubercles on the vertex (also in *Xylographus*), but the pronotal apex is never modified. The genus occurs throughout the Palaearctic and Indo-Pacific regions, with a single species occurring in the northern part of North America.

Octotemnus laevis Casey

Octotemnus laevis Casey, 1898: 91; Blatchley, 1910: 901 (dist., biol.); Dury, 1917: 27 (dist., biol.); Gibson, 1917: 150 (dist.); Gibson, 1918: 113 (dist.); Weiss and West, 1920: 8 (dist., biol.); Blackman and Stage, 1924: 86 (biol.); Graves, 1960: 66 (biol.). Type locality: "Rhode Island." Holotype, ♂, Casey Coll., USNM.

Octotemnus denudatus Casey, 1898: 91; Gibson, 1915: 137 (dist.); Dury, 1917: 27 (syn.); Weiss and West, 1920: 8 (dist., biol.); Fall, 1926: 200 (dist.); Hatch, 1962: 235, pl. 48, fig. 9 (dist., biol.). Type locality: California. Holotype, ♂, Casey Coll., USNM.

Distribution. Widespread throughout the northern part of North America, from southern Alaska to Quebec and Nova Scotia, south along the Pacific Coast to Monterey County, California, in the Sierra Nevada to Tulare County, in the Midwest to southern Iowa and Kansas, and on the East Coast to Alabama (Fig. 109). Marginal records: ALASKA: Skagway. BRITISH COLUMBIA: Terrace. ALBERTA: Edmonton. MANITOBA: Winnipeg. QUEBEC: St. Jean; Laniel. NOVA SCOTIA: Truro. ALABAMA: (no specific locality). MINNESOTA: Cormorant, Becker Co. MANITOBA: Aweme. ALBERTA: Cypress Hills. WASHINGTON: Kooskooskie, Walla Walla Co. CALIFORNIA: Dorset Camp, Sequoia National Park, Tulare Co.; Big Sur, Monterey Co.

Host fungi. Polyporus versicolor [86 (49)]; *Polyporus hirsutus* [11(1)]; *Polyporus pubescens* [7(4)]; *Lenzites betulina* [6(2)]; *Polyporus conchifer* [5(4)]; *Ganoderma applanatum* [5(1)]; *Polyporus abietinus* [1]; *Polyporus adustus* [1]; *Polyporus albellus* [1]; *Polyporus galactinus* [1]; *Polyporus pargamenus* [1]; *Polyporus squamosus* [1]; *Polyporus sulphureus* [1]; *Stereum* sp. [1].

Discussion. This species is easily distinguished by the ovoid body form, spinose tibiae, 8-segmented antennae, subconical procoxae with incomplete intercoxal process, vestiture of very short, fine hairs and scattered long fine hairs, and the triangular flap covering the abdominal fovea in the male. In *Rhopalodontus americanus,* the prosternum and male abdomen are similar, but the body is more elongate and parallel-sided, the tibiae spinose at the apices only, the antennae 10-segmented, and the vestiture of long, fine hairs only.

Octotemnus laevis is closely related to and possibly conspecific with *Octotemnus glabriculus* (Gyllenhal) of the Palaearctic region. The range is typically northern and the species is not very common in the Southeast. This is one of the most common species breeding in *Polyporus versicolor* and its relatives. Like *Cis fuscipes,* it appears to be equally common in the Northeast and on the Pacific Coast.

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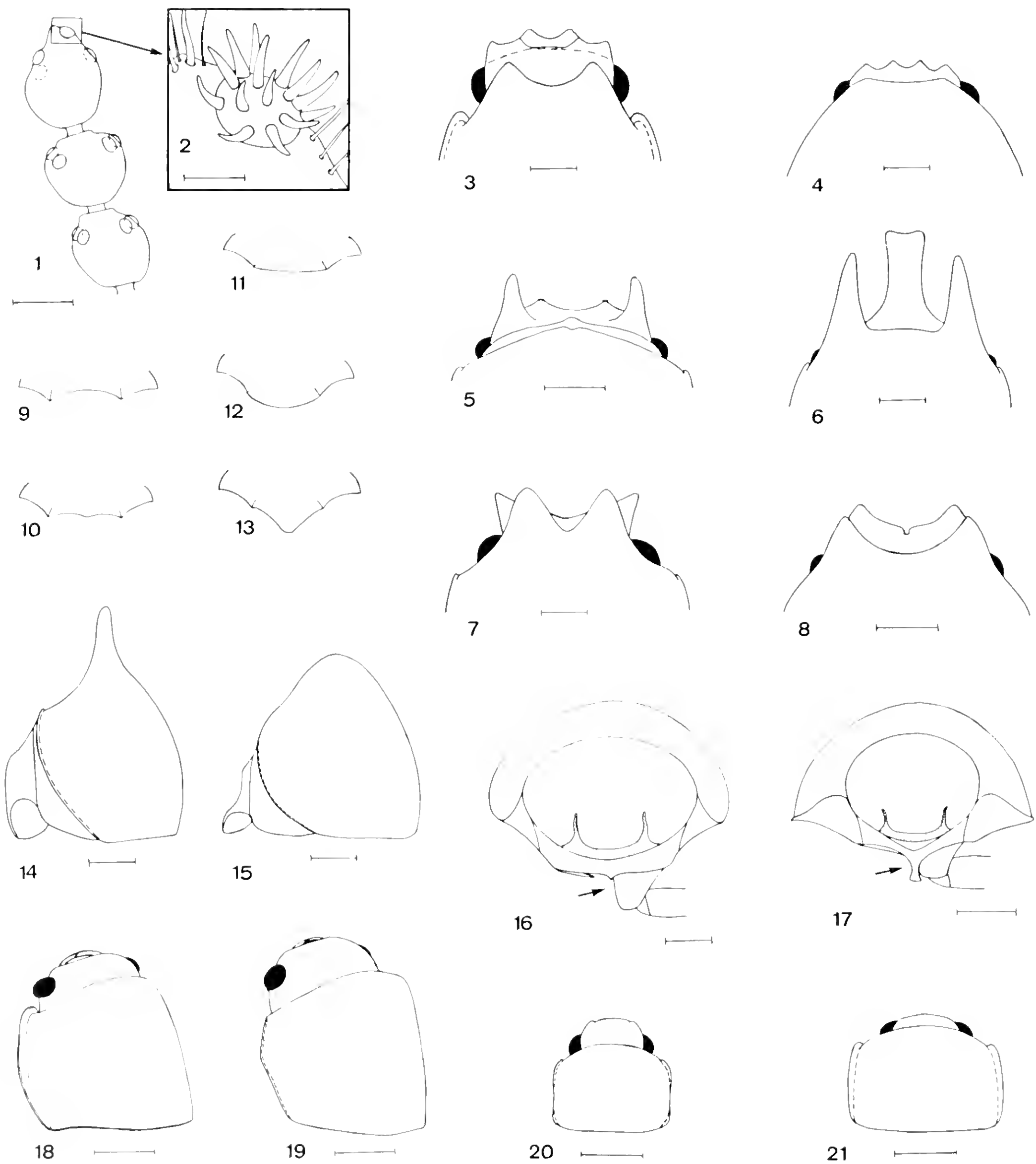
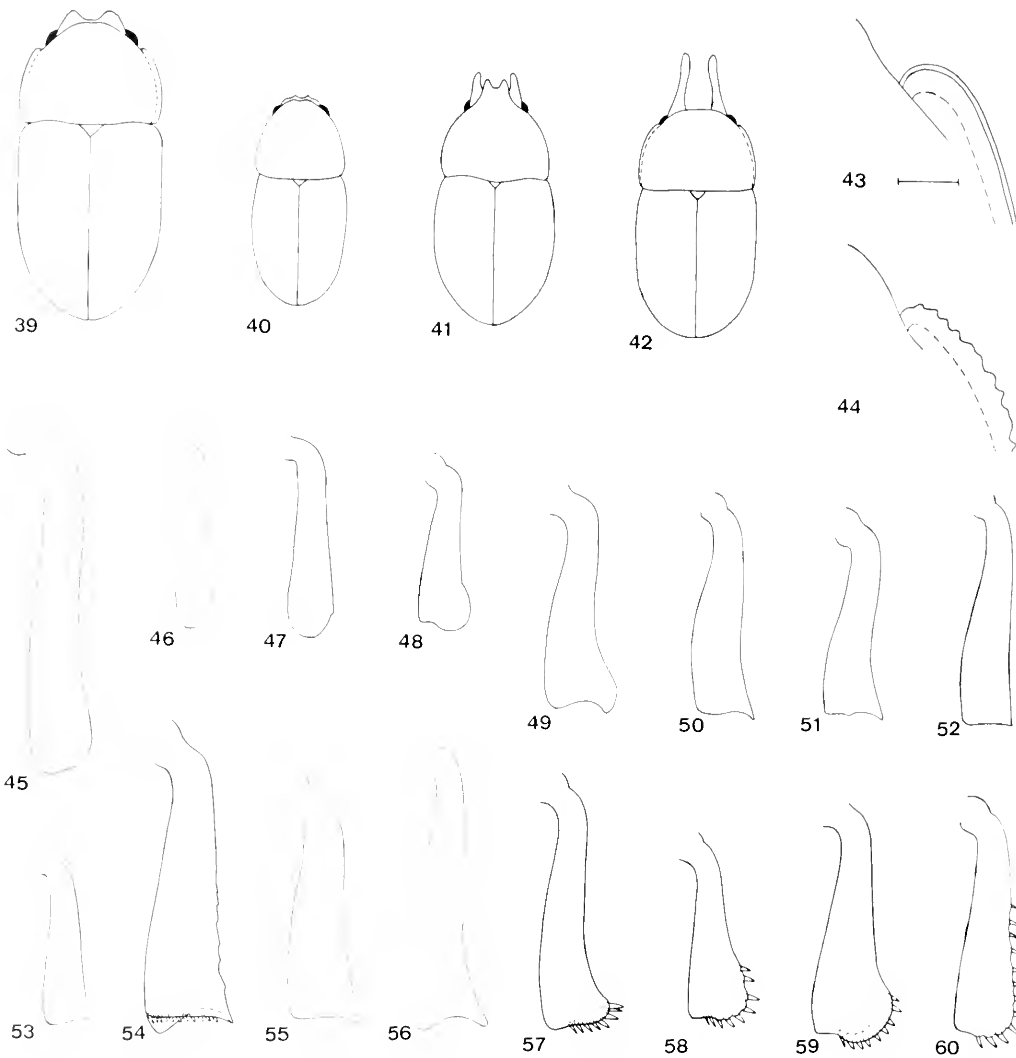
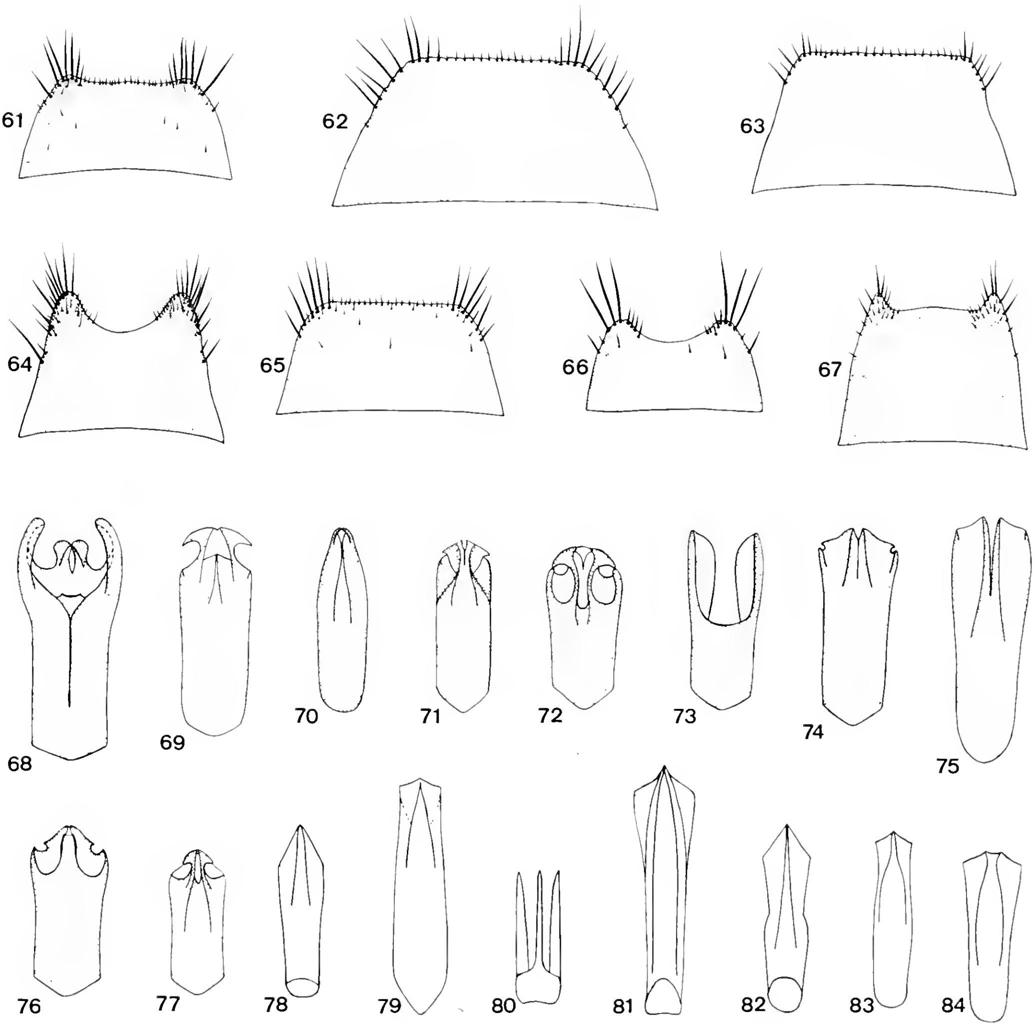


Fig. 1. *Cis vitulus* Mannerheim, antennal club [.076 mm]. 2. Same, section of terminal club segment, showing sensillifer [.018 mm]. 3. *C. vitulus* Mannerheim, head and pronotal apex of male, dorsal view. 4. *Plesiocis cribrum* Casey, same. 5. *C. niedhauki*, n. sp., same [.125 mm]. 6. *C. miles* (Casey), same [.125 mm]. 7. *C. Castlei* (Dury), same [.125 mm]. 8. *Ennearthron aurisquamosum*, n. sp., same [.125 mm]. 9–13. Diagrammatic cross-sections of prosternum and hypomera, showing concave, biconcave, flat, tumid, and carinate prosterna. 14. *Strigocis opacicollis* Dury, prothorax of male, lateral view [.125 mm]. 15. *Sulcacis lengi* Dury, same [.125 mm]. 16. *Octotemnus laevis* Casey, prothorax, anterior view [.125 mm]. 17. *Cis fuscipes* Mellié, same. 18. *Orthocis punctatus* (Mellié), head and pronotum, dorsolateral view. 19. *O. longulus* Dury, same. 20. *Hadraule elongatula* (Gyllenhal), head and pronotum, dorsal view. 21. *H. explanata*, n. sp., same. Unless otherwise indicated, 1 line = .250 mm.

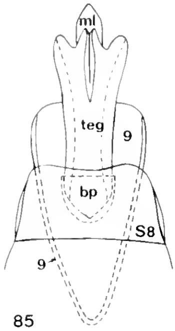
Figs. 22–28. Prothorax of male, ventral view. 22. *Orthocis punctatus* (Mellié). 23. *Cis fuscipes* Mellié. 24. *Ceracis thoracicornis* (Ziegler). 25. *Rhopalodontus americanus*, n. sp. 26. *Cis vitulus* Mannerheim. 27. *Malacocis brevicollis* (Casey). 28. *Hadraule blaisdelli* (Casey) [.125 mm]. 29. *Cis crinitus*, n. sp., section of elytral surface, showing long, erect, dark bristles and short, decumbent, light hairs. 30. *Cis horridulus* Casey, same, showing longer, erect and shorter, inclined bristles. 31. *Rhopalodontus americanus*, n. sp., abdomen of male, ventral view. 32. *Cis tetracentrum* Gorham, same. 33. *Octotemnus laevis* Casey, pectus (meso- and metathorax), ventral view [.125 mm]. 34. *Cis vitulus* Mannerheim, same. 35. *Ceracis similis* Horn, pronotal apex of male, dorsal view. 36. *Ceracis schaefferi* Dury, same. 37. *Orthocis huesanus* Kraus, head of male, anterodorsal view [.125 mm]. 38. *Orthocis punctatus* (Mellié), elytral apices, posterodorsal view. Unless otherwise indicated, 1 line = .250 mm.



Figs. 39–42. Outline of male, dorsal view (all drawn to same scale). 39. *Cis megastictus*, n. sp. 40. *C. stereophilus*, n. sp. 41. *C. rotundulus*, n. sp. 42. *C. cornelli*, n. sp. 43. *C. tetracentrum* Gorham, anterior angle and lateral margin of pronotum, dorsal view (1 line = .063 mm). 44. *C. discolor*, n. sp., same. 45–60. Right tibia of male, posterior view (all drawn to same scale). 45. *Orthocis punctatus* (Mellié). 46. *Dolichocis manitoba* Dury. 47. *Cis festivulus*, n. sp. 48. *C. cayensis*, n. sp. 49. *C. robiniophilus*, n. sp. 50. *C. cornelli*, n. sp. 51. *C. rotundulus*, n. sp. 52. *C. acritus*, n. sp. 53. *C. stereophilus*, n. sp. 54. *C. levettei* (Casey), showing apical spines. 55. *C. megastictus*, n. sp. 56. *C. discolor*, n. sp. 57. *Malacocis brevicollis* (Casey). 58. *Ceracis thoracicornis* (Ziegler). 59. *Rhopalodontus americanus*, n. sp. 60. *Octotemnus laevis* Casey.



Figs. 61–67. Abdominal sternite VIII of male [all drawn to same scale]. 61. *Cis robiniophilus*, n. sp. 62. *C. discolor*, n. sp. 63. *C. acritus*, n. sp. 64. *C. megastictus*, n. sp. 65. *C. festivulus*, n. sp. 66. *C. stereophilus*, n. sp. 67. *C. carnelli*, n. sp. 68–77. Tegmen of aedeagus [all drawn to scale]. 68. *C. discolor*, n. sp. 69. *C. tristis* Mellié. 70. *C. strialatus* Casey. 71. *C. robiniophilus*, n. sp. 72. *C. festivulus*, n. sp. 73. *C. acritus*, n. sp. 74. *C. megastictus*, n. sp. 75. *C. americanus* Mannerheim. 76. *C. carnelli*, n. sp. 77. *C. stereophilus*, n. sp. 78–84. Median lobe of aedeagus, outline only [all drawn to same scale]. 78. *C. megastictus*, n. sp. 79. *C. carnelli*, n. sp. 80. *C. acritus*, n. sp. 81. *C. discolor*, n. sp. 82. *C. stereophilus*, n. sp. 83. *C. robiniophilus*, n. sp. 84. *C. festivulus*, n. sp.



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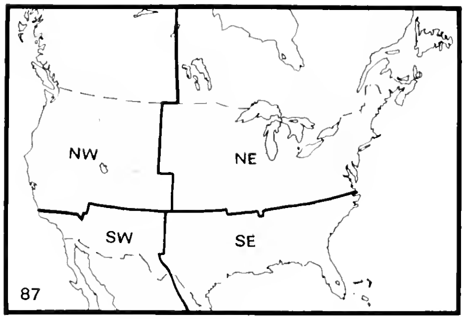

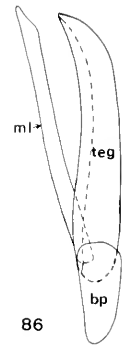

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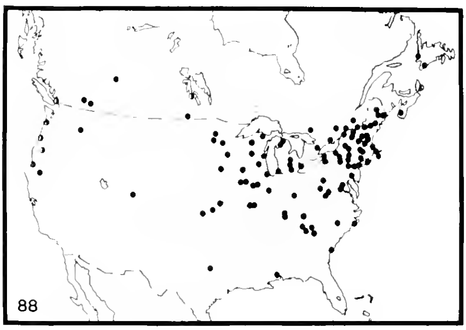
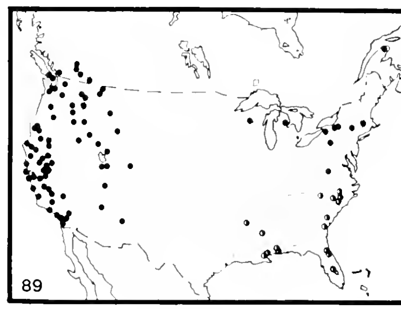
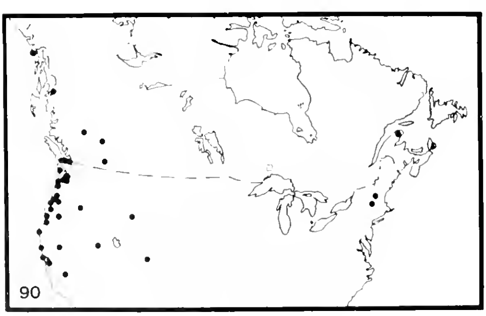






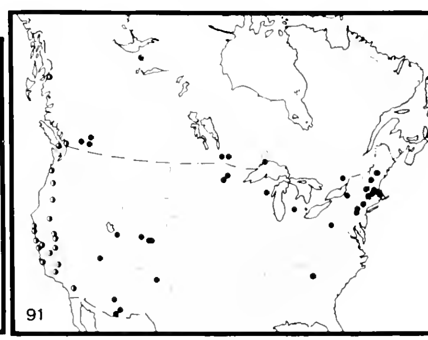
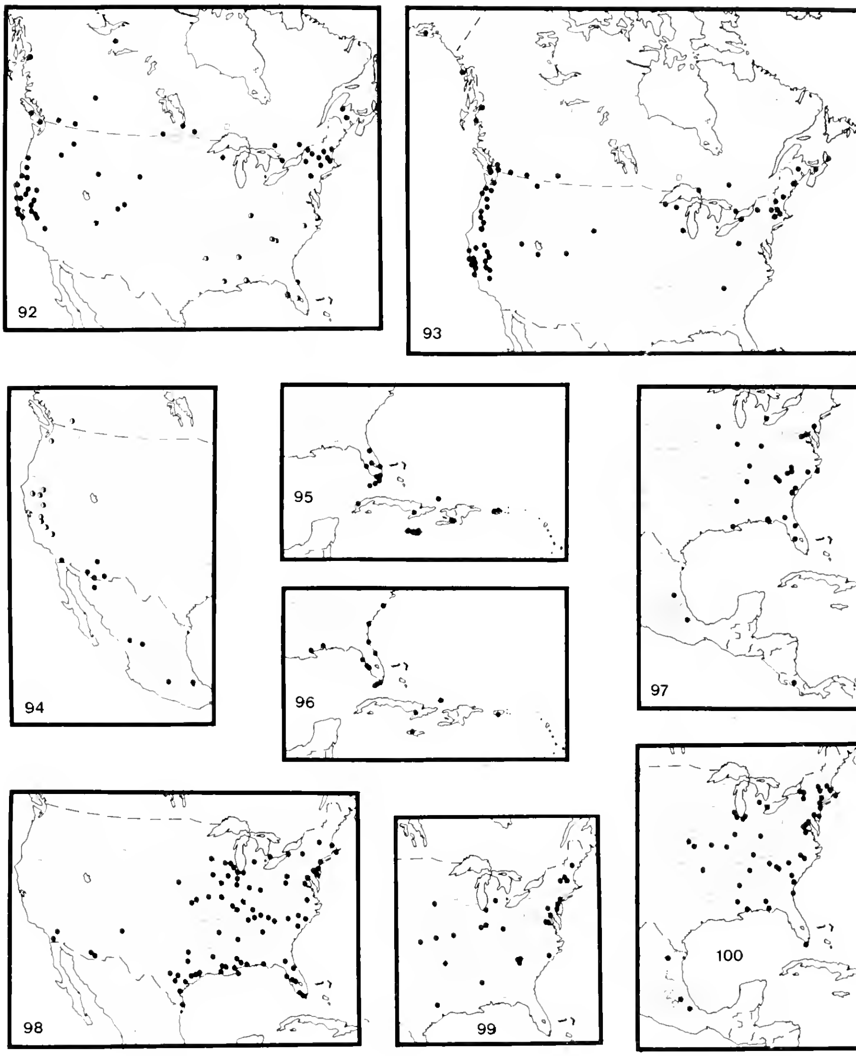
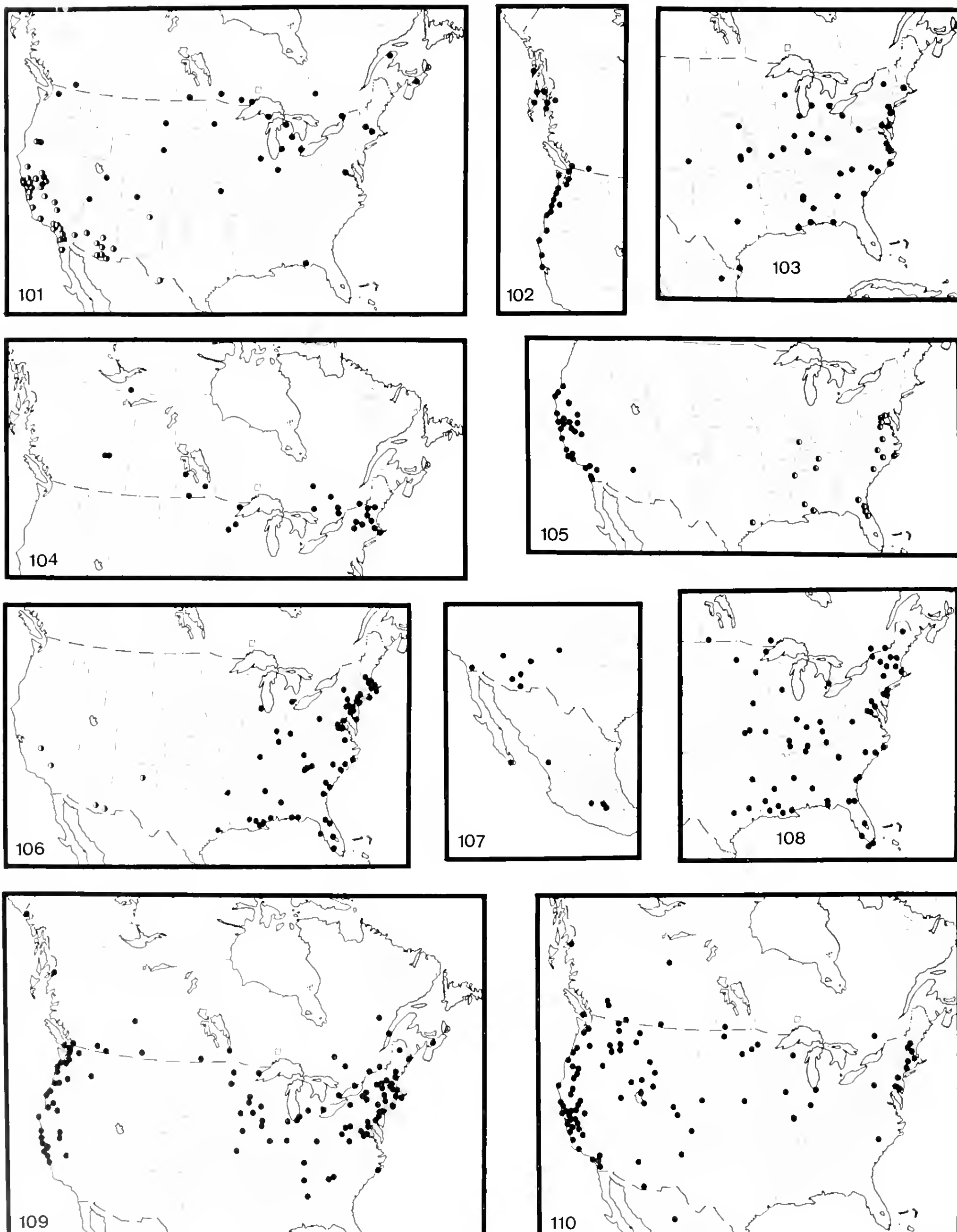


Fig. 85. Diagram of terminal abdominal segments and aedeagus, ventral view. 86. Diagram of aedeagus, lateral view. 87. Map of four regions of North America discussed on p. 432 and Tables 2 and 3. 88–91. Distribution maps. 88. *Cis levettei* (Casey) [full dot] and *C. maritimus* (Hatch) [half dot]. 89. *Plesiocis cribrum* Casey [full dot] and *Cis rotundulus*, n. sp. [half dot]. 90. *Cis ephippiatus* Mannerheim. 91. *Cis horridulus* Casey [full dot] and *C. hystriculus* Casey [half dot]. [S8 = sternite VIII; 9 = segment IX or genital ring; bp = basal piece; teg = tegmen; ml = median lobe.]



Figs. 92–100. Distribution maps. 92. *Dolichacis manitoba* Dury [full dot] and *Cis ursulinus* Casey [half dot]. 93. *Cis americanus* Mannerheim. 94. *C. tetracentrum* Gorham [full dot] and *C. angustus* Hatch [half dot]. 95. *C. hirsutus* Casey. 96. *C. crinitus*, n. sp. 97. *C. castlei* (Dury). 98. *C. creberrimus* Mellié [North American localities only]. 99. *Sulcacis lengi* Dury. 100. *Strigocis opacicollis* Dury.



Figs. 101–110. Distribution maps. 101. *Cis striolatus* Casey [full dot] and *C. versicolor* Casey [half dot]. 102. *C. biarmatus* Mannerheim. 103. *C. tristis* Mellié. 104. *C. pistoria* Casey. 105. *C. vitulus* Mannerheim [full dot] and *C. congestus* Casey [half dot]. 106. *C. subtilis* Mellié [full dot] and *C. acritus*, n. sp. [half dot]. 107. *C. duplex* Casey. 108. *Malacocis brevicollis* (Casey). 109. *Octotemnus laevis* Casey. 110. *Sulcacis curtulus* (Casey).